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Grevillea hortiorum Olde (Proteaceae: Grevilleoideae: Hakeinae), an uncommon species from winter-damp woodlands in the Avon Wheatbelt, south-west Western Australia

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Abstract

Grevillea hortiorum Olde is here described as a new species. It is a member of the *Triloba* Group *sensu* Flora of Australia, based on shared morphological characters, and it may be related to *Grevillea acrobotrya* Meisn. Numerous morphological differences distinguish it as a species, but its relationships have not been tested with phylogenetic data. Subsequent to its initial discovery, when it was thought to be rare, both its distribution and knowledge of populations have been greatly expanded, almost exclusively due to the efforts of its eponymous collectors. It was initially thought to be uncommon and associated with open wandoo woodland, but later collections have been gathered in open heath as well. An interim key to *Grevillea hortiorum* is provided.

Introduction

Grevillea hortiorum Olde is a new member of the *Triloba* Group *sensu* Makinson (2000), Group One *sensu* Olde & Marriott (1994), a moderately large entomophilous group of species, the size of which is being rapidly increased by new discoveries (e.g. Olde 2020). The *Triloba* Group can be characterised by its actinomorphic perianths, the tepals of which first separate below the limb, then at anthesis curl down before dis-cohering separately, by its thread-like, usually elongate pedicels, its pre-anthetic, antrorsely folded gynophore, its pistils contracted above the ovary and below an abrupt stylar dilation that tapers into the style-end, and by its erect, pollen-presenter. Two members of the *Triloba* Group (*G. acrobotrya* and *G. anethifolia*) included in a molecular phylogeny were unsurprisingly found by Mast *et al.* (2015) to be sister to each other. Together they are sister to two species in Group 8, *sensu* Olde & Marriott, the closest of which is *G. dielsiana* C.A.Gardner. However, all four were resolved in a large heterogeneous clade with species from 20 other morphological groups *sensu* Olde & Marriott, including *Finschia* Warb. Infra-clade relationships require further analysis, which will necessitate sampling of a greater number of species and utilising a larger set of molecular markers. The *Triloba* Group is presently under revision and as new species are recognised, genetic material is being added to existing datasets for further analysis. A full key to the Group will be provided when all currently known species are described, but an interim key is provided here. Terminology follows McGillivray and Makinson (1993); Olde and Marriott (1994); and Olde (2020).

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The documentation of rare flora and discovery of undescribed plant and insect species in many genera near to Perth has been an invaluable contribution, over many years, of retired teacher-lecturers, Fred Hort and wife Jean, to natural history science. Using their own initiative, they studied aerial photos of the region around Perth, then targeted search areas in which the vegetation appeared different from surrounding areas. This simple but effective approach has yielded numerous undescribed plant species and extended the ranges of many others (e.g. Thiele 2010, 2019; Obbens 2012; Hislop 2013).

Interim key to distinguish *Grevillea hortiorum* from other species in the *Triloba* Group

1 Fruits smooth; perianth limb reddish-brown or chocolate

2 Foliage dimorphic, the under-surface of vegetative leaves exposed; pollen-presenter fusiform ..... ***G. acrobotrya***

2* Foliage monomorphic; the under-surface of all leaves enclosed by margins; pollen-presenter conical ..... ***G. hortiorum***

1* Fruits not smooth; perianth limb lemon to yellow ..... See Makinson (2000: 415–419)

As noted above, a revised key to the remainder of the *Triloba* group is required, but many additional taxa are likely to be recognised, so provision of a full key to species is considered premature.

Taxonomy

Grevillea hortiorum Olde, **sp. nov.**

Type: Western Australia: Gunapin Ridge Road, Gunapin State Forest, west of York, *F. Hort 308*, 18 Nov 1998 (holo: PERTH 5235421; iso: CANB 511311, *n.v.*).

Diagnosis: Similar to *G. acrobotrya* Meisn., but differing in its leaves unimorphic, deeply dissected with the leaf under-surface enclosed by margins, not dimorphic with basal vegetative leaves obovate-cuneate and the under-surface exposed; common bracts longer (1–1.2 mm *vs* 0.5–0.9 mm), floral rachises longer (15–17 mm *vs* 9–13 mm long), pedicels longer (11–12.5 *vs* 5–9 mm long); more conspicuous stylar dilation; pollen-presenter wider at base than the style-end *vs* fusiform.

Grevillea sp. Gunapin (F. Hort 308), in Western Australian Herbarium (1998–). https://florabase.dpaw.wa.gov.au/browse/profile/18635 (accessed 28 Nov. 2020)

Seedlings not seen. Mature plant an erect, open, somewhat fastigiate, seed-obligate, stenobasic *shrub* 1.7–3 m high, 1–1.3 m wide, branching low to the ground from a smooth, grey trunk, sometimes bushy at the base with weakly emergent floral branches. *Branchlets* 1–2 mm thick, slender, greenish to yellowish-white, angular, usually with numerous fine longitudinal ribs decurrent from the petioles, glabrous, glaucous to caesious, rarely white sericeo-tomentose with a mixture of evanescent, appressed and ascending hairs of medium length; floral branches virgate with few side branches. *Adult leaves* divided, 1–3 cm long, 1–3 cm wide, polymorphic, ovate in gross outline, usually crowded, ascending to spreading, shortly petiolate, with primary and secondary orders of division, usually bi- or divaricately tri–5-sect, often biternate; leaves on floral branches not reduced in size; new growth light green, usually sericeous, with short evanescent white hairs, sometimes glabrous; *basal internode* 3.5–4.5(–8) mm long, 0.5–0.8 mm wide, monomorphous, linear, trigonous in cross-section; glabrous; *primary lobes* 3, spreading; *terminal and central lobes* similar; *ultimate leaf lobes* 0.5–1(–2.1) cm long, 0.5–0.8 mm wide, spreading, linear-subulate, trigonous to ellipsoid in cross-section, straight, the lobes often unequal; *apices of lobes* attenuate, spinescent, pungent; *spine* 1.2–2 mm long, necrotic with brown base, straight; *margins* smoothly to slightly angularly revolute; *adaxial surface* flat to slightly convex, smooth, sometimes channelled beside the obscure to prominent midvein, mostly glabrous or with scattered appressed biramous hairs; *abaxial surface* bisulcate, the lamina obscured by margins, glabrous or with a few scattered biramous hairs on the prominent midvein; *sulcae* 0.03–0.05 mm wide, packed with straight hairs; *texture* coriaceous; *petioles* 1–2 mm long, 1.2 mm wide, glabrous, normal, most scarcely wider than the leaf base, 3-merous, the central segment dominant but without extension down the branchlet, lateral segments closely aligned and poorly developed, the adaxial surface concave. *Conflorescences* simple or branched, glabrous except the bracts with ciliate margins, terminal, subterminal, occasionally a few axillary, sessile to very shortly pedunculate, scarcely to not exceeding the subtending leaf lobes; *terminal and subterminal conflorescences* simple to 5-branched; *axillary conflorescences* simple; *unit conflorescences* 2–2.5 cm long, 2 cm wide, subglobose to shortly cylindrical, 18–22 flowered; *buds* not seen; *peduncles* 0–2 mm

long; *floral rachises* 15–17 mm long, the apex without obvious vegetative extension, erect, usually straight, stout at base with distal tapering; *rachis nodes* prominent; *peduncular bracts* absent; *involucral bracts* not seen; *common bracts* 1–1.2 mm long, 0.3 mm wide, linear-lanceolate, caducous at early bud stage. *Flower colour*: Perianth and pedicels white, the perianth limb often greenish but becoming ultimately reddish-chocolate; pollen white *Flowers* acroscopic, scarcely to not nectariferous, fragrant, entomophilous, glabrous except where noted; *pedicels* white, 11–12.5 mm long, ascending to strongly erect; *basal pedicels* 11–12.5 mm long, *distal pedicels* 12–12.5 mm long; *torus* 0.5 mm across, oblique at 30–45º; *nectary* evident, angularly V-shaped, rising 0.1–0.15 mm above torus, margin entire. *Pistil* 4–4.5 mm long; *gynophore* 1.5–1.8 mm long, antrorsely folded before anthesis; *ovary* 0.5–0.65 mm long, 0.6–0.7 mm wide, lateral, round to broadly ellipsoid with truncated base sometimes slightly compressed laterally, remaining smooth after fertilisation; *style* constricted above the ovary, then swollen; *stylar constriction* 0.2–0.25 mm long, 0.2 mm wide, incurved or straight; *stylar swelling* 1.5–1.7 mm long, 0.3–0.4 mm maximum width, before tapering gradually below the style-end to 0.25–0.3 mm; *pollen-presenter* 0.65–0.7 mm long, narrowly ampulliform-conical; *base* 0.4–0.5 mm wide, abruptly divergent from the style-end, slightly oblique and sometimes irregular, not rimmed; *stigma* c. 0.15 mm wide, transverse. *Perianth* 3.5 mm long, 0.4–1 mm wide, actinomorphic; *perianth tube* 2 mm long, 0.7 mm wide, narrowly obovoid, contracting slightly just below the limb; *limb* 1.2 mm long, 1.5–1.7 mm wide, broadly ellipsoidal to round, usually the apex depressed; *tepals* 4 mm long, 0.7 mm maximum width, 0.5 mm wide below the limb; *abaxial surface* faintly to prominently ribbed; *adaxial surface* smooth; *tepal-limbs* 1.2 mm long, 1 mm wide, with prominent midrib. *Fruits* follicular, monospermous, 8–10 mm long, 4–6 mm wide, oblong-ellipsoidal, transverse to very oblique on incurved gynophore, with attachment subposterior, 2–3 mm from base; *persistent style* lateral, oblique with pollen-presenter conical; *pericarp* 0.5 mm thick along the suture, the thickness ± uniform throughout; *exocarp* smooth to slightly colliculose; *mesocarp* crustaceous; *endocarp* smooth, membranaceous.

Summary of diagnostic characters: *Grevillea hortiorum* is distinguished by the following combination of characters: stenobasic, weakly dimorphic habit, bushy at base with emergent, slender floral branches; branchlets usually glabrous, glaucous; leaves monomorphous, divaricately lobed with primary and/or secondary orders of division; leaf lobes spreading, subulate, ±uniform throughout, the abaxial surface not exposed; common bracts early caducous; pedicels 11–12.5 mm long; pistils glabrous, 4–4.5 mm long, with distinct stylar dilation; pollen-presenter not fusiform, slightly bulbous-conical, its base wider than the style; perianth glabrous, actinomorphic with chocolate globose limb; exocarp smooth to slightly colliculate.

Distribution: Western Australia, where known from a few scattered locations west of York and near Bindoon. It occurs in the Northam, Toodyay and York LGAs in the Avon Wheatbelt P2 and Northern Jarrah Forest IBRA Subregions of the Avon Wheatbelt and Jarrah Forest IBRA Regions.

Phenology: Flowering occurs from late winter to spring. Fruiting period: late spring

Habitat and ecology: Grows in wandoo or marri open woodland or in open winter-damp heath or thick scrub surrounded by woodland, on white or brown granite sand, clay-loam either combined with or over laterite. Recorded in association with a range of Proteaceae and other genera, including *Adenanthos cygnorum*, *Allocasuarina humilis*, *Banksia armata*, mallee *Eucalyptus* spp., *Grevillea bipinnatifida, G. scabra*, *G. pilulifera, Hakea gilbertii*, *H. incrassata*, *H. undulata*, *Hibbertia hypericoides*, *Isopogon divergens*, *Lasiopetalum exiguum*, *Petrophile ericifolia*, *P. striata* and *Xanthorrhoea preissii*.

Conservation status: *G. hortiorum* is known from several populations, some small, on disturbed roadsides and in natural bushland. Recently discovered populations near Bindoon contain thousands of plants and there does not appear to be an immediate conservation imperative. Several populations occur in designated Nature Reserves.

Etymology: Named for Frederick D. Hort (4 July 1937–) and frequent field companion, TAFE lecturer and amateur nature photographer, Jean L. Hort (née Boyle) (8 Feb 1952–). Before his retirement, Fred Hort was principal of Mt. Helena Primary School and had a keen interest in orchids and photography. Both have been dedicated volunteers at PERTH and their boundless enthusiasm for collecting and plant hunting has resulted in the discovery of this and several other previously unknown plant species.

Variation: Two specimens of *G. hortiorum* have been collected from plants with hairy branchlets. The specimen (*F. Hort* 1139) occurred on a disturbed roadside verge with three other plants of the same species bearing glabrous, glaucous branches. It was destroyed by roadworks in September 2001. The second (*Olde* 06/01 *& F. Hort*) was collected in an anthropogenically undisturbed population. In both cases no closely related species could be found nearby from which a hybridisation event could be inferred. Equally the specimens appear to have no population base. Accordingly, they are here treated as unexplained genetic variants without taxonomic significance.

Discussion: *Grevillea hortiorum* is similar to *G. acrobotrya* in its dimorphic habit, and in its flowers with similar reddish-chocolate perianth-limb. *Grevillea acrobotrya* differs however in its dimorphic habit, its leaves polymorphic, the vegetative leaves spreading, petiolate, non-pungent, obovate-cuneate, the margins dentate, and with the abaxial surface clearly exposed, the leaves on emergent floral branches erect, sessile and close-appressed to the branchlet, pungent, reduced in size with deeply sect-division, mostly trisect with the abaxial surface enclosed by margins. All leaves of *G. hortiorum* are similar, with trisect division and the under-surface enclosed by tightly revolute margins. *G. acrobotrya* also has shorter common bracts (< 1 mm long), shorter pedicels (5–9 mm long), and generally shorter pistils (3–3.5)–4 mm long) with a scarcely dilated style and fusiform pollen-presenter (i.e. the style-end and the base of the pollen-presenter merge seamlessly with only slight dilation). *Grevillea roycei* McGill. has similar glabrous, glaucous branchlets to *G. hortiorum* but differs in the shape of its pollen-presenter which is broader at the base than its height, and in its retrorse stem-clasping, basal leaf lobes and in its lemon-yellow perianth limb. *Grevillea levis* Olde & Marriott might also be confused. It differs from *G. hortiorum* in its unimorphic habit, its leaves with the basal internode 5–7 mm long, its ultimate leaf lobes 0.5–2 (–4) cm long, its common bracts 0.5 mm long, its perianth limb lemon to yellow, its pedicels 5–7 mm long. At the type locality *G. levis* is rhizomatous but is elsewhere not always so. *Grevillea levis* is currently under revision and further taxa may be identified.

Specimens examined: WESTERN AUSTRALIA: Gunapin State Forest, West York, *F. Hort 234a,* 21 Sep 1998 (PERTH); Wambyn Rd., Northam, *F. Hort 1136*, 21 Sep 2000 (PERTH); Mokine Nature Reserve, Northam, *F. Hort 1135*, 21 Sep 2000 (PERTH); Boyercutty Road, York, *F. Hort 1138,* 21 Sep 2000 (CANB, PERTH); Qualen Rd., West York, *F. Hort 459a*, 7 May 1998 (PERTH); Mokine Road, York, *F. Hort 1139, 21 Sep 2000* (PERTH, CANB); Julimar Proposed Conservation Park, Munyerring Block, Toodyay: in the NE cnr of Munyerring, 31°22'30" S 116°18'32"E, *F. Hort 2679 & B. Hort. s.n.*, 2 Nov 2005 (PERTH); Bindoon Training Area, Toodyay, *c.* 1 km ESE of Teds Crossing track, *F. Hort 2703*, 13 Nov 2005 (PERTH); Bindoon Training Area, 6.6–7.2 km SE–E from Artillery Road along the southern boundary, *F. Hort* 2673 *J. Hort* & *B. Hort*, 6 & 21 Oct 2005 (PERTH); Southern boundary of Bindoon Army Training Area, 6.6–7.7 km E from Artillery Rd., *P. Olde* 06/01 & *F. Hort,* 21 Jun 2006 (NSW, PERTH); Qualen Rd., West York, *P.M. Olde 99/153a & N.R. Marriott*, 21 Oct 1999 (NSW); Gunapin Forest Block, Gunapin Ridge Rd., West York, *P.M. Olde 99/154 & N.R. Marriott*, 21 Oct 1999 (NSW); Munyerring Spring Road North, beside Bindoon Army fence, Toodyay West, *P.M. Olde 15/47, K. Alcock, F. & J. Hort*, 15 Aug 2015 (NSW).

Fig. 1. *Grevillea hortiorum* with tiny native bee pollinator hovering. Photo: F. & J. Hort.

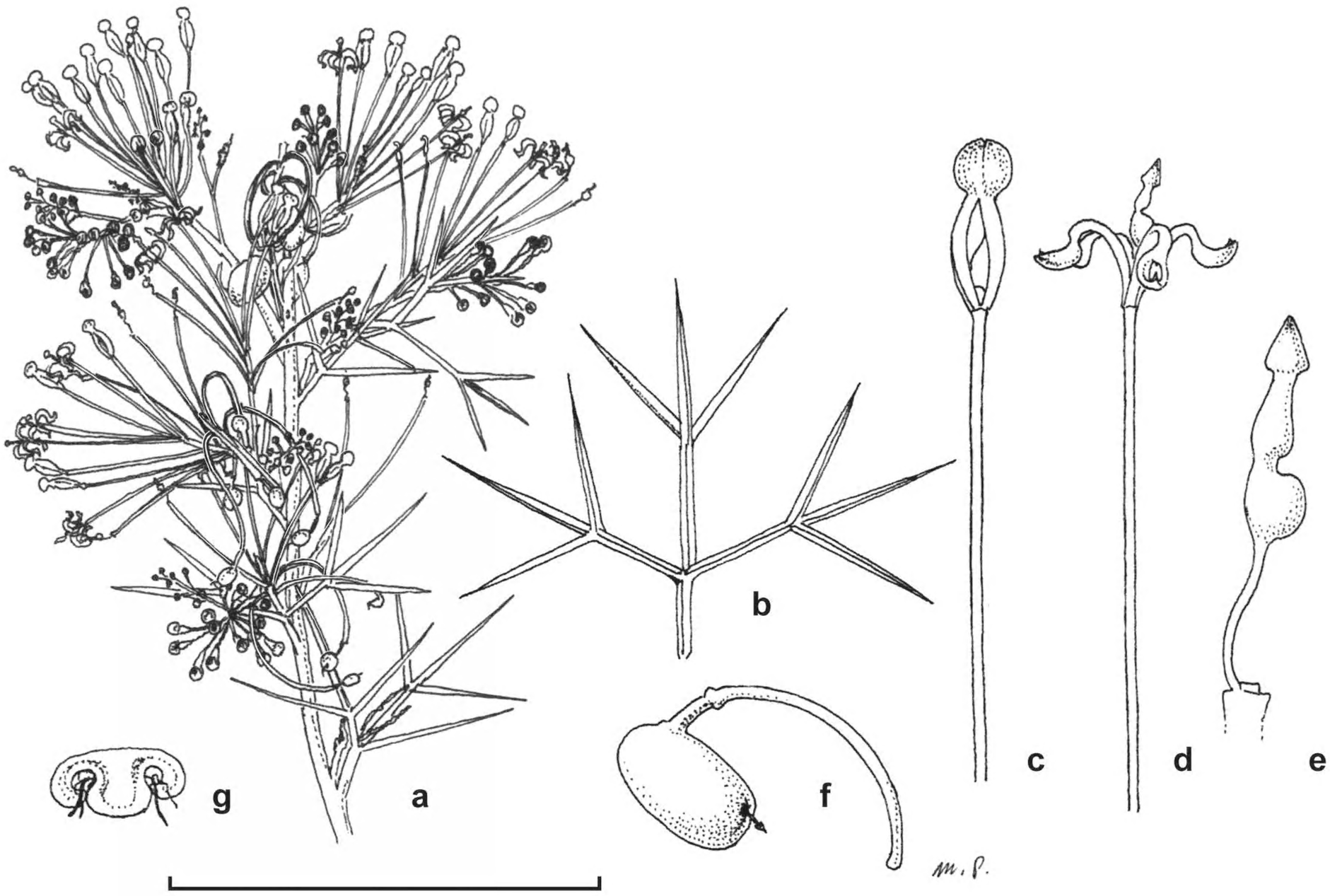

Fig 2. *Grevillea hortiorum*. a. habit; b. leaf; c. flower bud before anthesis; d. flower after anthesis; e. pistil. F. fruit; g. leaf cross-section. Scale bar: a = 50 mm; b, f = 25 mm; c, d = 12.5 mm; e = 6.25 mm; g = 2.5 mm. Illustration by M. Pieroni from material provided by F. & J. Hort.

Fig 3. *Grevillea hortiorum* in natural habitat. Photo J. & F. Hort.

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References

Hislop M (2013) A taxonomic update of *Conostephium* (Ericaceae: Styphelioideae: Styphelieae). *Nuytsia* 23: 313–335. https://florabase.dpaw.wa.gov.au/science/nuytsia/680.pdf

McGillivray DJ, Makinson RO (1993) Grevillea, *Proteaceae: a taxonomic revision*. (Melbourne University Press: Carlton, Victoria)

Obbens FJ (2012) Three new species of *Calandrinia* (Portulacaceae) from the Eremaean and South West Botanical Provinces of Western Australia. *Nuytsia* 22: 351–362. https://florabase.dpaw.wa.gov.au/science/nuytsia/640.pdf

Olde PM (2020) *Grevillea pieroniae* Olde (Proteaceae: Grevilleoideae: Hakeinae), a rare new species in the *Triloba* Group from the Stirling Range, Western Australia, and a short history of the group. *Telopea* 23: 227–235. http://dx.doi.org/10.7751/telopea14783

Olde PM, Marriott NR (1994) *The Grevillea Book*, Volume 1. (Kangaroo Press: Kenthurst, New South Wales)

Thiele KR (2010) *Darwinia hortiorum* (Myrtaceae: Chamelaucieae), a new species from the Darling Range, Western Australia. *Nuytsia* 20: 277–281. https://florabase.dpaw.wa.gov.au/science/nuytsia/597.pdf

Thiele KR (2019) A revision of the *Hibbertia commutata* (Dilleniaceae) species group. *Australian Systematic Botany* 32: 71–109. https://doi.org/10.1071/SB18007

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Taxonomic revision of *Corynotheca* (Hemerocallidaceae / Asphodelaceae)

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Abstract

The genus *Corynotheca* F.Muell. ex Benth. is revised and *Corynotheca borealis* R.L.Barrett, Keighery & T.Macfarlane is described as a new species from the east Kimberley region of Western Australia and the adjacent Northern Territory. *Corynotheca dichotoma* (F.Muell.) F.Muell. ex Benth. is reinstated for a species growing on yellow sands in the Mid West of Western Australia. The taxonomic and geographic limits of varieties of *C. micrantha* (Lindl.) Druce are reconsidered and all are recognised at specific rank. Four new combinations are made: *Corynotheca divaricata* (R.J.F.Hend.) R.L.Barrett & T.Macfarlane, *Corynotheca elongata* (R.J.F.Hend.) R.L.Barrett & T.Macfarlane, *Corynotheca gracilis* (R.J.F.Hend.) R.L.Barrett & T.Macfarlane and *Corynotheca panda* (R.J.F.Hend.) R.L.Barrett & T.Macfarlane. All are illustrated and a revised key to the thirteen species of *Corynotheca* recognised is provided.

Introduction

Classification of the lilioid monocots has undergone significant revision in recent decades (see Chase *et al.* 1996; Rudall *et al.* 2000; Rudall and Chase 1996 for reviews). A robust delimitation of Asparagales based on molecular phylogenetic data was presented by Fay *et al.* (2000), and subsequent refinements have generally focussed on the placement of particular genera, and the recognition of definable families. Hemerocallidaceae has been promoted as a useful family in many publications, though with varying circumscription (e.g. Clifford *et al.* 1998), and is still recognised by some (e.g. Boatwright and Manning 2010; Kaigongi 2020). Clifford and Conran (1998) included *Corynotheca* F.Muell. ex Benth. in Johnsoniaceae, a clade now accepted as belonging within the Hemerocallidoideae, and there is a growing acceptance of a broadly defined Asphodelaceae (formerly Xanthorrhoeaceae; sensu APG IV, 2016, see Klopper *et al.* 2013), including subfamily Hemerocallidoideae (Chase *et al.* 2000, 2009; Givnish *et al.* 2018).

Corynotheca is here recognised as a genus of thirteen species, all endemic in Australia. Phylogenetic data place *Corynotheca* as sister to a clade including *Arnocrinum* Endl. & Lehm, *Caesia* R.Br., *Johnsonia* R.Br.,

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Hodgsoniola F.Muell. and *Hensmania* W.Fitzg. (the Johnsonioid clade), and related to *Tricoryne* R.Br., genera with a number of general similarities in floral morphology and most genera having arillate seeds (Clifford and Conran 1998; McPherson *et al*., 2004; Devey *et al*. 2006; Wurdack and Dorr 2009; Seberg and Peterson 2012; Steele *et al*. 2012; Chen *et al*. 2013; McLay and Bayly 2016; Givnish *et al*. 2018). The Johnsonioid clade is endemic to Australia, except for a few species of *Caesia* in southern Africa (Boatwright and Manning 2010). Detailed phylogenetic studies based on nuclear and chloroplast markers and complete plastome data are underway that also support a relationship between *Corynotheca* and the Johnsonioid clade (A. Webb, J. Birch and B. Gunn, pers. comm.).

Corynotheca is unique in the Johnsonioid clade in the following characters: leaves are caducous (quickly withering); the inflorescences are large and persistent, giving a shrub-like appearance, and commonly divaricate; anthers dehisce introrsely (Clifford and Conran 1998). The aril on the seed is unusual, with only four 'shrubby' *Caesia* species (*C. arcuata* T.Macfarlane, Conran & C.J.French, *C. rigidifolia* F.Muell., *C. viscosa* Keighery and *C.* sp. Great Victoria Desert (C. Tauss 2835)) having similar arils (Macfarlane *et al*. 2020a). A closer relationship with *Arnocrinum* is possible, the two genera sharing 6 stamens with alternately long and short staminal filaments, though in *Arnocrinum* the tepals are purple, fused to a greater degree (±half their length), the anthers are connate, forming a tube around the style and the reticulately ornamented seeds lack an aril (Keighery 1987a; Clifford and Conran 1998). Chromosome numbers appear to be indicative of relationships as *Corynotheca*, *Caesia* and *Tricoryne* all appear to have an ancestral basic chromosome number of $n = 7$, while *Arnocrinum* is based on $n = 6$ (Keighery 1984; Clifford and Conran 1998), so *Corynotheca*, with $2n = 42$, appears to have undergone a chromosome duplication event. *Arnocrinum* has retained a base chromosome number of $2n = 24$ while two *Caesia* species have $2n = 28$ and 56 respectively, suggesting a chromosome duplication event within *Caesia*. To date, relatively few species have been studied, and additional counts may prove informative.

Corynotheca, *Caesia* and *Tricoryne* all occur in temperate, tropical and arid Australia, though individual species are almost universally restricted to a single biome. *Corynotheca* has a rhizomatous habit, with often shrub-like perennial stems that are usually more or less leafless and both capsular and nut like fruits *Caesia* is perhaps the most 'lily'-like genus, with an annually replaced basal rosette of leaves and tuberous roots in most species, and most are drought avoiders, dying back to the underground root tubers. Four 'shrubby' *Caesia* species (noted above) have tough leaves that dry up, leaving the green stem to perennate; roots that may be more or less uniformly thickened or narrowly dauciform; and have *Corynotheca*-like arillate seeds. They use the stored food in their root tubers to resprout after fire. These are also annually replaced, and store starch (Pate and Dixon 1983). Tuber morphology (distally or evenly swollen roots) appears to define two major groups within *Caesia*. *Tricoryne* contains a group of leafy species with tuberous roots that store starch, but these may not die back in summer, although the green stems may replace the leaves as the photosynthetic unit as many species are summer flowering.

Members of the genera *Corynotheca* and *Tricoryne* have parallel adaptions as a group of leafless rhizomatous species where the perennial stems have replaced the leaves as the photosynthetic unit. Members resprout from buds on the rhizome after fires. They also produce numerous long slender roots, which may aid nutrient acquisition, rather than the short thick or tuberous roots produced in *Caesia*. Although both genera have colonized and speciated on the sandy inland soils, *Corynotheca* species are more widespread in the arid zone of inland Australia. *Caesia* species and the tuberous *Tricoryne* species have primarily colonised rocky habitats. Most of these species in *Tricoryne* are currently unnamed and are represented in *FloraBase* by phrase names (Western Australian Herbarium 1998–).

In *Corynotheca*, *Caesia* and *Tricoryne*, flowers are diurnal, lasting a single day and the perianth twists after flowering. All members observed are pollinated mainly by small, solitary bees (Figure 11 D–F), although wasps and flies (Figure 16 F) also visit the flowers, but appear to be less efficient pollinators (G.J.Keighery, pers. obs.). All members tend to occur in dense populations and open only a limited number of flowers per plant at a time. While most species of all genera observed in cultivation or in bushland can self-pollinate on flower closure, capsule set following selfing is uniformly low, to almost zero, compared to very high set following cross-pollination (G.J.Keighery, pers. obs.).

Corynotheca flowers are white and bowl shaped, with readily available nectar, but little is known of their pollination biology. Most members of *Caesia* have white or blue, open bowl shaped flowers with readily available nectar. These are visited by bees from the genera *Lasioglossum* Curtis, *Leioproctus* Smith and *Nomia* Latreille. *Caesia* sp. Wongan (K.F. Kenneally 8820) has become effectively buzz pollinated by *Leioproctus* bees, having reflexed, blue perianth lobes, yellow anthers clustered around the style and no apparent nectar. *Tricoryne* is the exception in this group of genera, with large yellow flowers having hairy anther filaments. While a small amount of nectar is produced, most bees concentrate on pollen collecting, with the nectar at the

base of the flowers usually ignored, perhaps obscured by the dense anther filament hairs. Although *Tricoryne* is visited by bees for pollen, the anthers are not buzzed as claimed in some texts, the anthers dehiscing by longitudinal slits (G.J. Keighery, pers. obs.).

Members of the genus *Caesia* have capsular fruits which dehisce to release shiny or dull black seeds with a papery, cap-like aril that are ant dispersed in the few species observed (*C. micrantha*, *C. occidentalis* and *C. setifera*; G.J.Keighery, pers. obs.). Ant dispersal is a common feature of many Australian Asparagales. Some *Corynotheca* species retain a capsular (though eventually dehiscent) fruit that releases black seeds with a firm, white aril, but many can appear to have a nut-like fruit. These fall from the plants when mature, but there is no data on dispersal. The fruit of *Tricoryne* are schizocarpic, developing from the deeply divided ovary, and the seeds lack an aril, so they are quite distinct from single-seeded *Corynotheca* fruit.

Taxa now placed in *Corynotheca* were described by Brown (1810), Mueller (1859), Bentham (1878), Gauba (1948), and Henderson (1987). Nomenclatural changes within *Corynotheca* have been made by Endlicher (1846), Baker (1876), Bentham (1878), Druce (1917), Macbride (1918) and Henderson (1987). The taxonomic treatment by Henderson (1987) presented a major advance in our understanding of the genus *Corynotheca*, describing seven new taxa that are all recognised in this revision. Henderson (1987) often had only limited material available, noting that further study was warranted, and indicated that his new varieties might in future merit the rank of species, a finding we confirm here based on the examination of additional collections.

Many of Henderson's measurements and observations for particular taxa have been expanded based on more recent collections, but his taxonomic concepts have been little-modified by us in this paper, except for the recognition of two additional species and recognition of his varieties at specific rank. Henderson's original key did not account for the full range of variation found in *Corynotheca*, leading to numerous misidentifications, so a new key is provided below, with a similar framework. In addition to these taxonomic accounts, partial or regional accounts of *Corynotheca* have been provided by Mueller (1870), Bailey (1913), Black (1922, 1943), Eichler (1965), Cunningham *et al.* (1981), Jessop (1981, 1986), Macfarlane (1987), Bennett and Dundas (1988), Clifford *et al.* (1992), Rye (1992), McCune and Hardin (1993), Conran and Walsh (1994), Kenneally *et al.* (1996), Wheeler and Graham (2002), Barrett and Pin Tay (2016), Keeble (2017) and Eichler (2018).

Key features for identification of *Corynotheca* species include roots, rhizomes, stem branching patterns, leaves, inflorescence structure, tepal shape and size, anther filament colour and seed morphology, as described in the methods section below. The plasticity of many of these morphological characters (often in response to environmental conditions) makes speculation on relationships between most species based on morphology alone a tenuous exercise. It is possible that white *vs* yellow anther filaments divides the genus into two natural groups. All tropical species except *C. flexuosissima* have yellow anther filaments, while *C. divaricata*, *C. licrota* and *C. pungens* are the only species with yellow anther filaments that extend south of the tropic, all growing in relatively arid areas. The dense, perennial, shrub-like habit and ability to resprout rapidly after fire probably make *Corynotheca* species important habitat plants for invertebrates and small vertebrates.

The new species described in this revision builds on regional studies of Asparagoid monocot taxonomy in Western Australia (Macfarlane and Conran 2015; Macfarlane and Keighery 2015; Barrett 2018). This small genus exhibits interesting patterns of biogeography, and development of a comprehensive molecular phylogeny would be a rewarding exercise to determine the relationships and patterns of speciation within the genus. Like numerous Australian monocot genera (e.g. *Calectasia* R.Br., Barrett and Dixon 2001; Barrett and Barrett 2015; *Chaetospora* R.Br., Barrett *et al.* 2020; *Laxmannia* R.Br., Keighery 1987b; *Lepidosperma* Labill., Barrett and Wilson 2012; *Thysanotus* R.Br., Sirisena *et al.* 2016; Macfarlane *et al.* 2020b), the highest diversity of species is found in the south-west of Western Australia, inviting further research on the origins and diversification of these genera.

Methods

The descriptions are based primarily on dried herbarium material held at AD, BRI, CANB, MEL, NSW and PERTH. Historical specimens have been critical to understanding species concepts, and the determination of conservation priorities as there have been documented range reductions in species such as *C. acanthoclada* and the value or herbarium collections in this regard must be emphasised (Thomson *et al.* 2018; Raven and Miller 2020). All specimens have been seen unless otherwise noted. Where only images have been examined (either on https://plants.jstor.org or digital photographs supplied by individuals), these are indicated by '*'. Colour and shape of flowers is based on photographs and field observations, including collectors' notes.

Roots and rhizomes (true stems) are rarely collected but are useful to distinguish some species. Branching patterns differ between sections of growth. True stems are subterranean, lateral and short. Most, if not

all, species can re-sprout following fire. New growth following fire can be more elongate and less angular than regular growth, sometimes making identification more difficult if only regrowth material is collected. Following Clifford and Conran (1998), tall above-ground growth is interpreted as the inflorescence, so all the reduced foliage is interpreted as bracts, even though leaf-like in *C. pungens*. True leaves are poorly known as most species have only a few leaves arising from the subterranean stem that usually senesce prior to anthesis, so they are missing from most collections.

Primary inflorescence branches (including the peduncle) are usually erect, sometimes decumbent, and unbranched. Secondary stems are usually multi-branched and vary greatly between species in angle of divergence at nodes. Flowers develop on tertiary stems termed racemules, which also vary greatly between species in angle of divergence at nodes. A racemule is here interpreted as a single (ultimate) inflorescence branch produced on secondary stems. Angles of divergence at the nodes are measured as 'outside' angles from the continuing axis, so non-divergent stems continue at 180°, rather than being recorded as 0° divergence from the continuing axis. The determination of branching versus the continuing axis is based on the position of the bract. Sometimes the branch is at such an angle and thickness that it looks like it should be the axis, but the bract shows otherwise, the new branch developing between the bract and the continuing axis (Figure 1). The inflorescences structure, and the manner in which angles have been measured, are illustrated in Figure 1. Inflorescence branching patterns of representative species are shown in Figures 2–5.

The proportion of flowers developing per racemule is variable, even if the number of nodes is regular. While there are trends in particular species, leading Henderson (1987) to use this as a potential taxonomic character, this probably reflects environmental conditions during anthesis, with species from more arid areas commonly aborting most flowers but still developing most under ideal conditions.

As Henderson (1987) noted, fruit shape varies considerably depending on the number of seeds that develop. A maximum of three seeds have been observed in a single capsule, though development of up to six may be possible under ideal conditions. Most seeds are smooth and glossy until just before full maturity, when they become longitudinally striate, so observations of seed morphology need to carefully assess seed maturity. It appears that when multiple seeds develop in a single capsule, one seed may remain smooth, perhaps due to 'stunted' development. *Corynotheca divaricata* is the exception in the genus, with all seeds remaining smooth, or becoming very finely pitted. *Corynotheca licrota* may produce both smooth and striate seeds in a single capsule, but this might reflect the stage of development of individual seeds at the time of collection. While Henderson (1987) excluded the caruncle from seed length measurements, the caruncle is included here in the seed length measurement as sufficient mature seeds are now available for most taxa to obtain a reliable range of variation.

Corynotheca asperata R.J.F.Hend. is still poorly collected due to its remote distribution and some plant base, fruit and seed characters remain unknown.

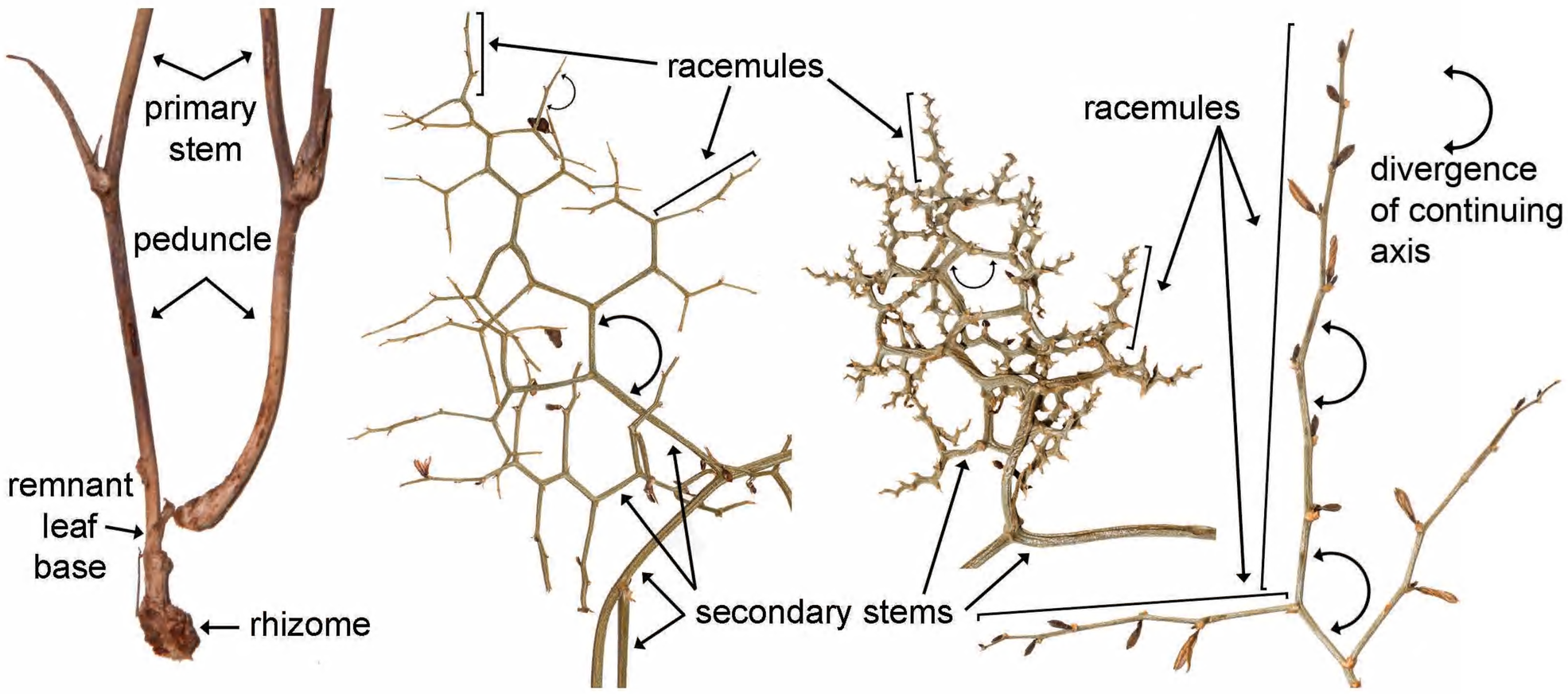

Fig. 1. Key features used in descriptions and for identification of *Corynotheca* species.

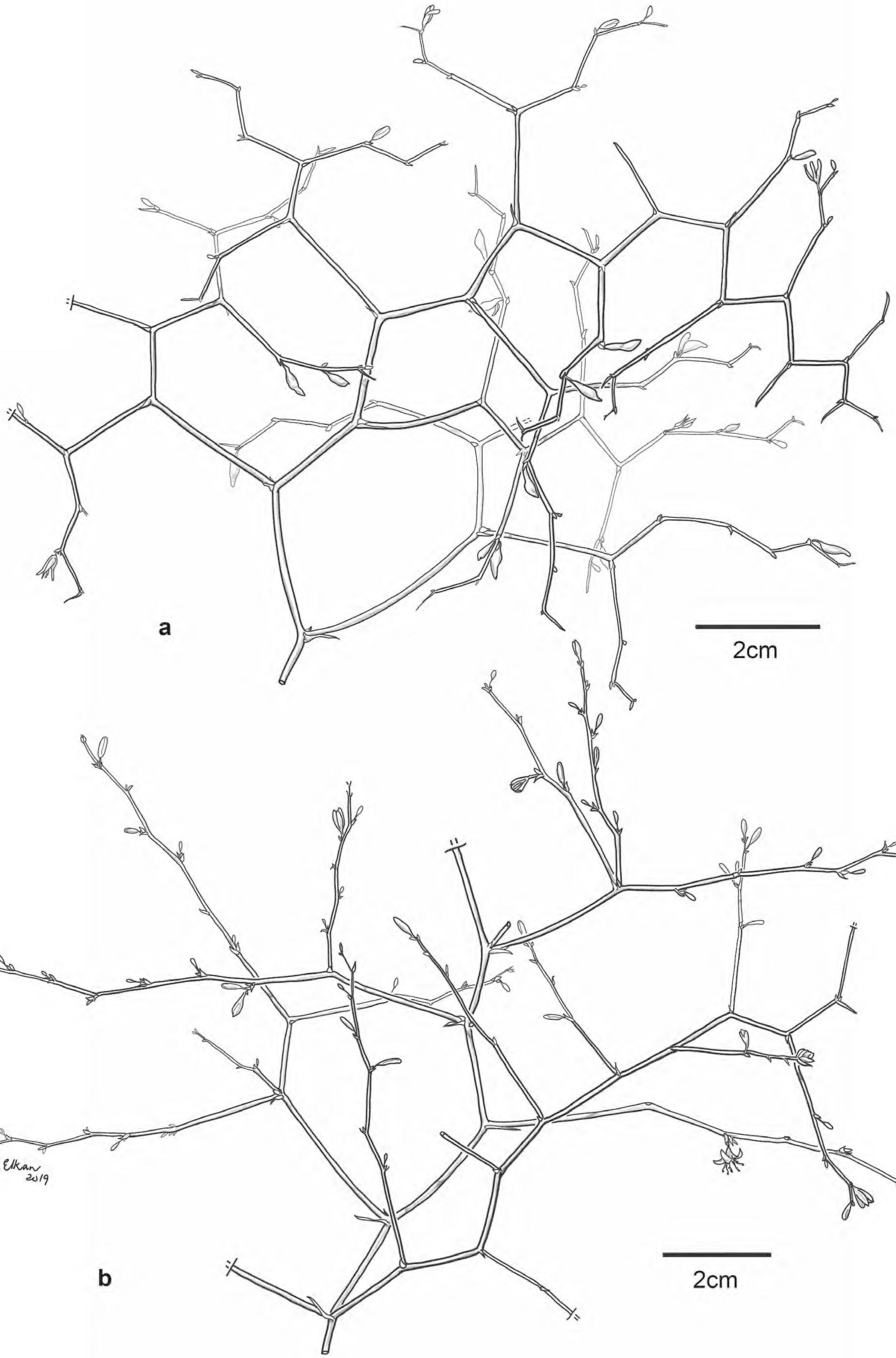

Fig 2. Line illustrations of *Corynotheca* branchlets. A. *Corynotheca divaricata* form 1. B. *Corynotheca divaricata* form 2. Vouchers: A: Waite Creek, *N. Henry 365* (NSW); B: Finke Settlement, *D.E. Albrecht 5640* (NSW). Illustrations by L. Elkan.

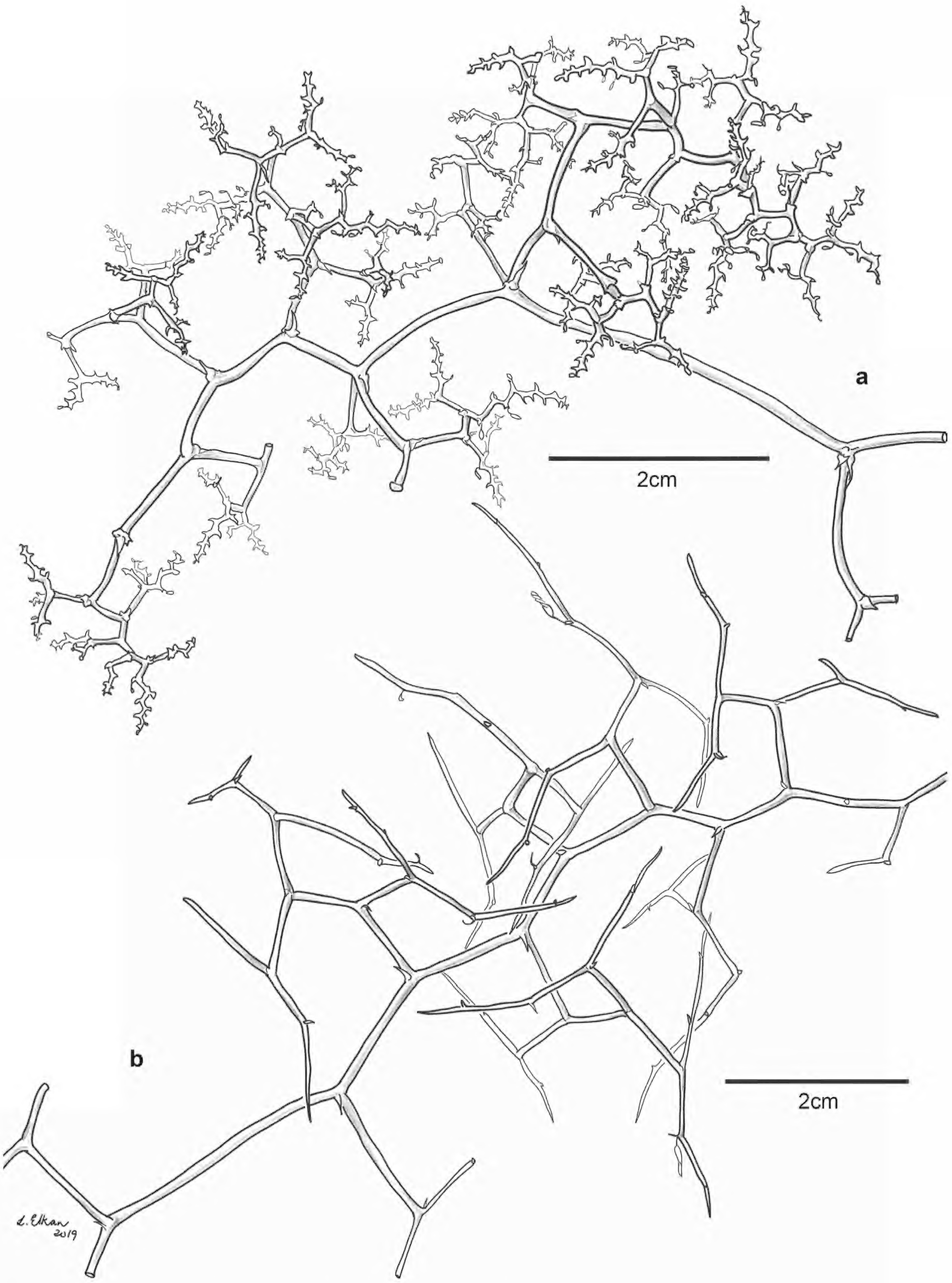

Fig. 3. Line illustrations of *Corynotheca* branchlets. A. *Corynotheca flexuosissima*. B. *Corynotheca micrantha*. Vouchers: A: Cape Range, *A.S. George 10309* (NSW); B: Gingin Brook, *N.T. Burbidge 8048* (NSW). Illustrations by L. Elkan.

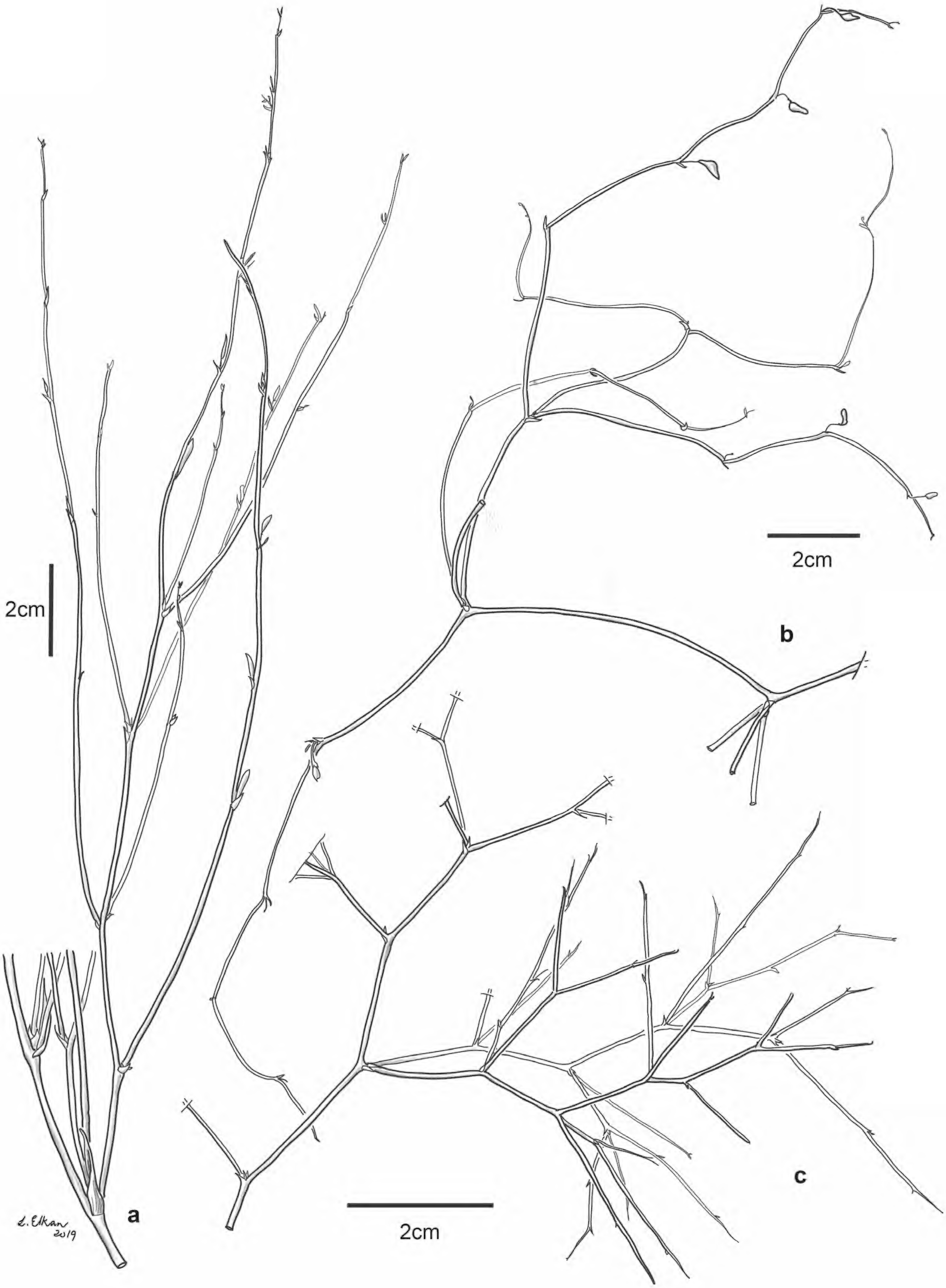

Fig. 4. Line illustrations of *Corynotheca* branchlets. A. *Corynotheca lateriflora*. B. *Corynotheca panda*. C. *Corynotheca gracilis*. Vouchers: A: Goyder River, *C.R. Dunlop 8680 & N.G. White* (NSW); B: Mount Arid, *A.N. Rodd 5144* (NSW); C: Dampier Peninsula, *E. Mjoberg s.n.* (NSW 109422). Illustrations by L. Elkan.

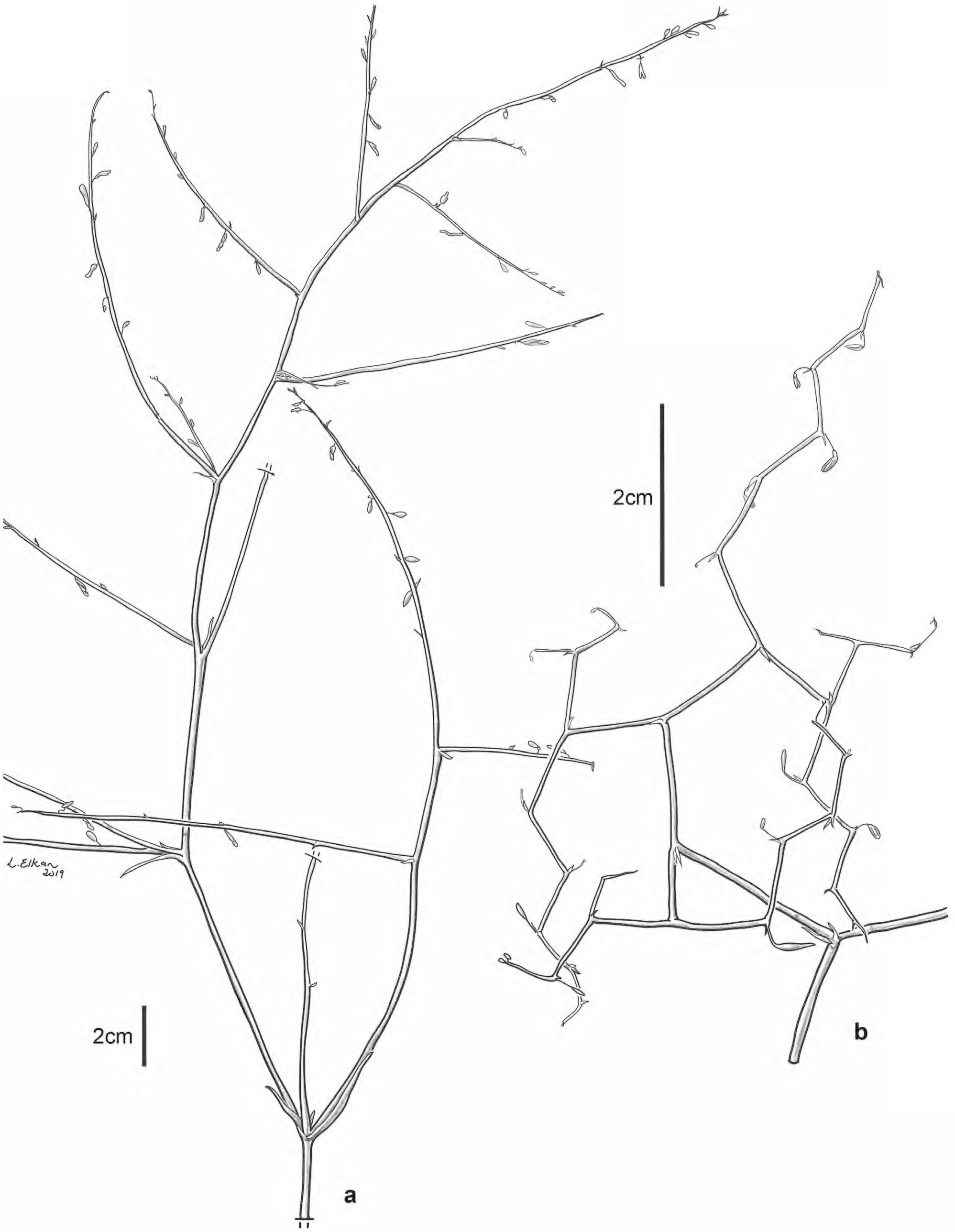

Fig. 5. Line illustrations of *Corynotheca* branchlets. A. *Corynotheca pungens*. B. *Corynotheca dichotoma*. Vouchers: Gascoyne River, *E.N.S. Jackson 3092* (NSW); B: Murchison River, *W.R. Barker 2191* (NSW). Illustrations by L. Elkan.

Taxonomy

Corynotheca F.Muell. ex Benth., *Fl. Austral.* 7: 49 (1878), *non* Ochyra (1990; Funariaceae).

Type species: *Corynotheca lateriflora* (R.Br.) Benth., designated by R.J.F.Henderson, *Fl. Austral.* 45: 473 (1987).

Caesia sect. *Corynotheca* F.Muell., *Fragm.* 1: 215 (1859), *nom. nud.*

Corynotheca F.Muell., *Fragm.* 7: 68 (1870), *nom. prov., nom. nud.*

Tufted, tangled, rhizomatous *perennials*, herbaceous or shrub-like, usually glabrous, occasionally scabrous. *Roots* many, fibrous or fleshy-fibrous, often sand-binding. *Stems* short, subterranean, perennial, bearing leaves and inflorescences. *Leaves* few, linear-subulate, flat or sometimes convolute, reducing rapidly to bracts upwards, all usually senesced by anthesis, but long and persistent in a few species, margins usually glabrous (sometimes scabrid hairs present on *C. pungens*). *Inflorescence* perennating, irregularly paniculate, interrupted, evenly diffuse, dark to dull green; peduncle erect to ascending, subterranean at base; major branches ±straight, erect, ascending or decumbent; panicle branches often ±divaricate; racemules with axis often tortuous, with 0–21 nodes, sometimes reduced to a spine-like axis, finely ribbed, but otherwise usually smooth, sometimes scabrid or crenulate; apex tapering and tip acute or ±pungent in two species; internodes ±straight to curved; flowers bisexual, ±regular, solitary or paired (rarely 3), and of different ages, in branch axils, pedicellate; lower bracts linear-subulate, acuminate, occasionally long and leaf-like; uppermost bracts obovate or ovate-attenuate to ±triangular or minute and needle-shaped. *Perianth* segments shortly connate at base, spirally twisting after anthesis, deciduous. *Sepals* narrowly elliptic to oblong or linear, apex apiculate, with tepal apex trichomes, white or pink to purplish to brown, median band darker, veins purplish to brown. *Petals* narrowly elliptic to oblong, acute or obtuse, white to cream to pale mauve or pink, median band darker, veins purplish to brown. *Stamens* 6, epipetalous; filaments straight or slightly incurving, sometimes kinked (commonly so when immature), alternately unequal or subequal and then the antepetalous ones longer, minutely papillose, white or yellow; anthers basifixed, introrse, becoming extrorse, dehiscing by longitudinal slits, yellow; pollen polychotomosulcate, triangular to rounded triangular, *c.* 17 μm diam. *Ovary* superior, 3-locular; ovules 2 per loculus, 1 erect, 1 pendulous; style filiform, shorter than, ±equal to or exceeding stamens; stigma capitate, minute. *Fruit* capsule-like and late-dehiscent or nut-like and irregularly rupturing, spreading to pendulous or antrorse, rarely ascending, obpyriform to clavate-attenuate, ovoid or obovoid, brown, usually slightly wrinkled. *Seeds* 1–3 per fruit, ellipsoidal, usually glossy black to iridescent, longitudinally striate or rarely smooth to very finely pitted; caruncle conical distally, the lobes free or fused.

Diagnostic characters: *Corynotheca* is distinguished from *Caesia* by subterranean stems with fleshy-fibrous roots (*vs* stem absent, roots fleshy or swollen), leaves usually rapidly senesced (persistent in a few species) the perennating inflorescences with a shrub-like appearance (*vs* annual), inflorescence many-branched and variously divaricate (*vs* ±racemose; not or few-branched and straight), short pedicels to 3.4 mm long (*vs* 3–15 mm long), capsules not or irregularly lobed (*vs* consistently 3-lobed) and ellipsoid seeds (*vs* globose) and seeds with a thick caruncle (*vs* a papery aril).

Distribution: A genus of 13 species, widespread across much of Australia, endemic, but absent from the far north-east and far south-east mainland (occurring only in the arid zones of Queensland, New South Wales and Victoria) and Tasmania.

Common names: Zigzag Lily, Sand Lily.

Etymology: The specific epithet is from the Greek *koryne* (a club) and *theke* (a case), in reference to the shape of the fruit.

Affinities: *Corynotheca* is generally assumed on morphological similarity to be most closely related to *Caesia* R.Br., sharing polychotomosulcate pollen (Furness *et al.*, 2014). The two genera differ as noted under diagnostic characters. Based on molecular phylogenetic data, these two genera belong in a clade that also includes *Arnocrinum*, *Hensmania*, *Hodgsoniola*, *Johnsonia* and *Stawellia*, this clade being sister to *Tricoryne*, a genus sometimes confused with *Corynotheca* in the absence of flowers, which differs in having bearded staminal filaments and yellow (rarely almost white) flowers. Four *Corynotheca* species assessed have $2n = 42$, while two *Caesia* species have $2n = 28$ or 56 respectively, and *Arnocrinum* has $2n = 24$ (Keighery 1984). These, and a number of related Australian genera, may be buzz-pollinated (Keighery 1984; Furness *et al.*, 2014).

Notes: *Corynotheca* species may form large clones in their favoured habitats. Excavation of stands of *C. flexuosissima* and *C. pungens* found that many plants are apparently connected by underground, spreading rhizomes (G.J.Keighery, pers. obs.).

Table 1. Morphological characters considered diagnostic for *Corynotheca* species and general distribution.

	acanthoclada	*asperata*	*borealis*	*dichotoma*	*divaricata*	*elongata*	*flexuosissima*	*gracilis*	*lateriflora*	*licrota*	*micrantha*	*panda*	*pungens*
Habit	erect to spreading	spreading	erect to spreading	spreading	spreading	spreading	spreading	spreading	erect	erect	spreading	spreading to decumbent	erect to spreading
Roots	fibrous	fibrous	not seen	fleshy-fibrous	fleshy-fibrous	fleshy-fibrous	fleshy-fibrous	fibrous	fleshy-fibrous	fibrous	fleshy-fibrous	fleshy-fibrous	fleshy-fibrous
Mature leaves	dry at anthesis	dry at anthesis	dry at anthesis	dry at anthesis	dry at anthesis	dry at anthesis	dry at anthesis	dry at anthesis	dry at anthesis	persistent, basal	dry at anthesis	dry at anthesis	persistent, mostly cauline, margins sometimes with scabrid hairs
Basal leaf length (often bract-like)	8–48 mm	<30 mm	6–25 mm	10–67 mm	14–68 mm	5–34 mm	12–23 mm	7–15 (–20) mm	(40–)120–220 mm	50–300 (–600) mm	28–105 mm	45–180 mm	40–110 mm
Basal leaf width	0.4–1.0 mm	not seen	0.4–0.7 mm	0.8–1.5 mm	1.6–2.9 mm	0.8–1.7 mm	0.6–1.1 mm	0.5–0.8 (–1.1) mm	0.6–2.2 mm	2.5–4.1 (–9) mm	0.6–1.6 mm	0.7–1.6 mm	0.5–2 mm
Basal leaf shape in section	flat	flat	flat	flat	flat	flat	flat	flat	flat to convolute	flat or complicate	flat	flat	flat
Panicle branch angle	170–180°	140–170°	90–160°	80–140°	90–140°	90–150°	80–150°	90–150°	90–150°	130–160°	80–150°	(90–)130–170°	90–150°
Racemule length	4–27 mm	4–23 (–50) mm	10–75 mm	15–60 mm	17–95 mm	37–78 mm	4–12 (–25) mm	20–60 mm	65–175 mm	75–300 mm	12–40 mm	18–106 mm	30–140 (–300) mm
Nodes per racemule	0 or 1	(0)1–6	1–5	(1–)5–13	5–8(–10)	4–8	(5–)9–20	2–5	4–7	5–17	2–4	(2–)5–8	5–21
Racemule branch angle	90–110°	140–180°	80–100°	80–110°	140–180°	(160–)170–180°	90–150°	110–140°	170–180°	±180°	130–180°	140–180°	170–180°
Racemule axis	finely scabrid	scabrid	smooth	smooth	smooth	smooth	smooth	smooth	smooth	smooth	smooth	smooth	smooth
Racemule internode length	2–4.5 mm, ±straight	2–11 mm, gently curving	5–11 mm, ±straight	1–7 mm, ±straight	4–13 mm, ±straight	4–13(–20) mm, ±straight	0.8–2 mm, straight to gently curving	5–23 mm, ±straight	7–31 mm, ±straight	4–24 mm, ±straight	4–12 mm, straight to gently curving	8–19 mm, ±straight to evenly curving	3–14 mm, ±straight
Racemule diam.	0.3–0.5 mm	0.5–0.7 mm	0.2–0.4 mm	(0.2–)0.4–0.6 mm	0.4–0.9 mm	0.2–0.5 mm	0.2–0.6 mm	0.2–0.4 mm	0.1–0.6 mm	0.4–1.3 mm	0.3–0.6 mm	0.3–0.7 mm	0.6–1.1 mm

	acanthoclada	*asperata*	*borealis*	*dichotoma*	*divaricata*	*elongata*	*flexuosissima*	*gracilis*	*lateriflora*	*licrota*	*micrantha*	*panda*	*pungens*
Upper bract apex	acuminate	acuminate	acuminate	acuminate	acute	acuminate	acuminate	acuminate	acuminate, sometimes stiff	acuminate	acuminate	acuminate	stiff, ±pungent
Flowers	1–3	solitary (or rarely paired?)	solitary	solitary	solitary or paired (rarely 3)	solitary	solitary	solitary	solitary	solitary (or rarely paired)	solitary	solitary or paired	solitary
Proportion of flowers developing	few–most	?few	?most	?most	most	?most	?few	few–most	most	most	most	?few	?few–most
Pedicel length	0.3–0.7 mm	0.3–0.8 mm	0.9–1.3 mm	0.8–2.3 mm	0.3–1.2 mm	0.8–1.9 mm	0.2–0.9 mm	1.0–3.1 mm	1.4–2.0 (–3.0) mm	1.2–2.6 mm	1.2–2.9 mm	1.3–2.9 (–3.4) mm	0.9–1.7 mm
Perianth length	1.5–1.7 mm	4.5–6.3 mm	3.9–5.0 mm	4.1–5.0 mm	4.5–5.9 mm	3.1–4.3 mm	1.4–2.1 mm	4.0–6.5 mm	6.5–8.0 mm	4.3–6.0 mm	2.8–4.5 mm	3.5–4.6 mm	2.7–6.1 mm
Staminal filaments	erect, subequal, white	not seen	slightly spreading, unequal, yellow	spreading, subequal, white	slightly spreading, unequal, yellow	erect, subequal, white	erect, subequal, white	slightly spreading, unequal, yellow	slightly spreading, unequal, yellow	slightly spreading, subequal, yellow	erect, subequal, white	slightly spreading, subequal, white	Erect to spreading, subequal to equal, yellow
Staminal filament length	0.6–0.7 mm	not seen	1.4–2.1 mm	2.2–2.7 mm	1.4–1.8 mm	1.8–2.5 mm	0.6–0.8 mm	1.9–4.0 mm	3.2–4.1 mm	1.7–2.2 mm	1.7–2.1 mm	1.7–2.0 mm	2.1–2.6 mm
Seed length	1.9–2.4 mm	not seen	3.8–4.2 mm	2.9–3.3 mm	2.3–3.7 mm	1.8–2.7 mm	1.8–2.1 mm	3.4–4.7 mm	5.0–6.8 mm	3.0–4.3 mm	2.3–3.4 mm	2.8–3.3 mm	2.7–2.9 mm
Caruncle lobes	fused, colliculate	not seen	fused, colliculate	fused, colliculate	fused, colliculate	fused, colliculate	fused, colliculate	fused, colliculate	free, colliculate	free, folded	fused, colliculate	fused, colliculate	fused, colliculate
Testa surface	striate	not seen	striate	striate	smooth to very finely pitted	striate	striate	striate	striate	smooth to finely striate	striate	striate	(smooth to) striate
Testa appearance	glossy	not seen	glossy	glossy	very glossy	glossy	glossy	glossy	glossy	glossy	glossy	glossy	glossy
Distribution	Kalbarri to Greenough, WA	Great Sandy Desert, WA; Tanami, NT	Karunji Station, WA to Keep River, NT	Mullewa, to Shark Bay and Dirk Hartog Island, WA	Wiluna, WA, central NT, N of SA, to Springvale SE Qld	Eneabba to Dunsborough, inland to Lake King, WA	Cape Range to Onslow, WA	Broome and Mandora to Ngumban Cliffs, to Kiwirrkura, WA	Top End, Gulf of Carpentaria, NT	Arid zone, WA, NT, SA, Qld, NSW, Vic.	Eneabba to Dunsborough, inland to Williams, WA	Blackwood River to Cape Arid, WA	Port Headland to Shark Bay, inland to Newman, WA

Corynotheca is one of numerous Australian Asparagoid genera with tepal apex trichomes (Macfarlane and Conran 2016). These structures are particularly well-developed in *Corynotheca*, forming a conspicuous hook-like subterminal appendage on the sepals (see flower images in this paper, e.g. Figs 14B, 17D). Henderson (1987) refers to them as adaxial appendages on the sepals and illustrates them in his Fig. 96E. Macfarlane and Conran (2016) suggest that these structures, which by adhesion between the trichomes of different sepals (and petals, where they are less conspicuous) hold the buds closed until anthesis, may function by controlling the timing or enhancing the rapidity of flower opening. *Corynotheca* species have more or less synchronous opening of flowers, often late in the day (Eichler 2018). In the only well-studied example of flower behaviour in a species with tepal apex trichomes, the Californian *Chlorogalum pomeridianum* (DC.) Kunth, Stockhouse and Wells (1978) suggested that rapid flower opening, which occurs at about the same time each day, may concentrate pollinator visitation and hence promote effective pollination and outcrossing.

Previous treatments have stated that anther filaments in *Corynotheca* are all of equal length, differing from *Caesia* in this regard, however field observations and photographs show that filaments are usually of two distinct lengths, or a few species are subequal. The thickened portion of the filaments is usually greater in the longest filaments, the shorter filaments often only being thickened in the lower half.

Caesia micrantha has similarly striate seeds, however other generic characters listed above readily separate this species from *Corynotheca*. Thickened caruncles are found in *Caesia viscida* Keighery and related taxa, which have superficially similar habits to *Corynotheca licrota*, but phylogenetic data place *Ca. viscida* within *Caesia s. str.* and *Co. licrota* within *Corynotheca s. str.* (A. Webb, B. Gunn and J. Birch, pers. comm.).

Table 1 presents a range of morphological characteristics useful for distinguishing between *Corynotheca* species.

Key to species of *Corynotheca*

1. Perianth 6.5–8.0 mm long; leaves (40–)120–220 mm long; seeds 5.0–6.8 mm long (Top end, Gulf of Carpentaria, NT)..... *C. lateriflora*

1: Perianth 1.4–6.5 mm long; leaves 5–110(–300) mm long; seeds 1.8–4.7 mm long 2

2. Inflorescence axes and racemules finely scabrid; pedicels 0.3–0.8 mm long (Great Sandy Desert, WA; Tanami, NT) ..... *C. asperata*

2: Inflorescence axes and racemules smooth, ribbed or crenulate; pedicels 0.8–2.9(–3.4) mm long (except for *C. flexuosissima*; pedicels 0.2–0.9 mm long and *C. divaricata*; pedicels 0.3–1.2 mm long) 3

3. Mature basal leaves persistent at anthesis, 2.5–4.1(–9) mm wide; racemules consistently continuous at ±180° (i.e. straight); caruncle lobes free (Arid zone, WA, NT, SA, Qld, NSW, Vic.) ..... *C. licrota*

3: Mature basal leaves mostly dry at anthesis, 0.6–2.2(–2.9) mm wide; racemules usually diverging at 80–170° (*C. elongata* & *C. pungens* often almost straight); caruncle lobes fused 4

4. Plants with mature cauline leaves not reduced to bracts, persistent, clustered in major axils, margins sometimes with scabrid hairs; upper bract apices stiff, ±pungent; racemules 0.6–1.1 mm diam. (Port Headland to Shark Bay, inland to Newman, WA) ..... *C. pungens*

4: Plants with leaves all basal, dry at anthesis, reduced to bracts above, margins glabrous; upper bract apices acuminate to acute, but not pungent; racemules 0.2–0.9 mm diam..... 5

5. Racemules 4–12(–25) mm long, with (5–)9–20 nodes, internodes 0.8–2 mm long, inflorescence with a dense, gnarled appearance; perianth 1.4–2.1 mm long (Cape Range to Onslow, WA)..... *C. flexuosissima*

5: Racemules (4–)10–300 mm long, with 0–8(–13) nodes, internodes 2–23 mm long; inflorescence open to somewhat dense, not gnarled; perianth 2.8–8.0 mm long 6

6. Seed testa smooth to very finely pitted; pedicels 0.3–1.2 mm long; basal leaves 1.6–2.9 mm wide (Wiluna, WA, central NT, N of SA, to Springvale SE Qld) ..... *C. divaricata*

6: Seed testa longitudinally striate; pedicels 0.8–2.9(–3.4) mm long; basal leaves 0.4–1.7 mm wide..... 7

7. Racemules with 0–5 internodes (always some <4) 8

7: Racemules with 4–13 internodes (always some >5)..... 11

8. Inflorescence branches stiff; racemules ±stiffly straight or sometimes diverging, pungent, 4–27 mm long (Kalbarri to Yandanooka (S of Mingenew), WA)..... *C. acanthoclada*

8: Inflorescence branches flexible, racemules slender, ±flexible, straight to diverging, not pungent, 10–75 mm long 9

9. Racemule internodes diverging at 130–180°, 0.3–0.6 mm wide; perianth 2.8–4.5 mm long; basal leaves 28–105 mm long; seeds 2.3–3.4 mm long (Eneabba to Dunsborough, inland to Williams, WA) ..... *C. micrantha*

9: Racemule internodes diverging at 80–140°, 0.2–0.4 mm wide; perianth 3.9–6.5 mm long; basal leaves 6–25 mm long; seeds 3.4–4.7 mm long 10

10. Racemule internodes diverging at 80–100°; pedicels 0.9–1.3 mm long; staminal filaments 1.4–2.1 mm long (Karunji Station, WA to Keep River, NT) ..... *C. borealis*

10: Racemule internodes diverging at 110–140°; pedicels 1.0–3.1 mm long; staminal filaments 1.9–4.0 mm long (Broome to Ngumban Cliffs, to Kiwirrkura, WA) ..... *C. gracilis*

11. Racemule with (1–)5–13 internodes, diverging at 80–110°, internodes 1–7 mm long (Mullewa, to Shark Bay and Dirk Hartog Island, WA) ..... *C. dichotoma*

11: Racemule with (2–)5–8 internodes, diverging or straight (140–180°), internodes 4–19(–20) mm long 12

12. Basal leaves 5–34 mm long; racemule internodes diverging at (160–)170–180°; internodes 4–13(–20) mm long, 0.2–0.5 mm diam., ±straight; seeds 1.8–2.7 mm long (Eneabba to Dunsborough, inland to Lake King, WA) ..... *C. elongata*

12: Basal leaves 45–180 mm long; racemule internodes diverging at 140–180°; internodes 8–19 mm long, 0.3–0.7 mm diam., ±straight to evenly curving; seeds 2.8–3.3 mm long (Blackwood River to Cape Arid, WA) ..... *C. panda*

Corynotheca acanthoclada (F.Muell.) F.Muell. ex Benth., *Fl. Austral.* 7: 50 (1878); *Caesia acanthoclada* F.Muell., *Fragm.* 1(9): 215 (1859); *Corynotheca micrantha* var. *acanthoclada* (F.Muell.) R.J.F.Hend., *Fl. Austral.* 45: 474 (1987).

Type: near Murchison River, Western Australia, *n.d.*, *A.F. Oldfield s.n.* [*?1095*] (lecto, first step designated by R.J.F.Henderson *Fl. Austral.* 45: 302, 474 (1987), second step designated here: MEL 107030; isolecto: K 000794729*, K 000794730*, K 000794731*, MEL 107029).

Tufted, tangled, rhizomatous *perennial*, glabrous. *Roots* several, 30–70 mm long, fibrous, not sand-binding. *Stems* short, to 10 mm long and 4 mm wide. *Leaves* few, linear-subulate, 8–48 mm long, 0.4–1.0 mm wide, flat, reducing rapidly to bracts upwards, all usually senesced by anthesis. *Inflorescence* perennating, irregularly paniculate, interrupted, evenly diffuse, to 37 cm long, olive-green; peduncle erect to ascending, subterranean at base; major branches ±straight, erect or ascending; lowest branch 0–1.5 cm from rhizome; panicle branches ±straight, each node divaricate at 170–180°; racemules with axis not tortuous, 4–27 mm long, with 0 or 1 nodes, each node diverging at 90–110°, but commonly reduced to a spine-like axis 4–27 mm long, ribbed to narrowly winged, very finely covered in blunt, scabrid hairs 0.05–0.15 mm long; apex tapering and tip pungent; internodes 2–4.5 mm long, 0.3–0.5 mm wide, ±straight; flowers 1–3 in branch axils, few–most developing; lower bracts linear-subulate, 3–15 mm long, acuminate; uppermost bracts obovate to ±triangular, 0.8–1.2 mm long; pedicels 0.3–0.7 mm long. *Perianth* 1.5–1.7 mm long, segments connate for *c.* 0.1 mm, spirally twisting after anthesis, deciduous. *Sepals* narrowly oblong, 1.5–1.7 mm long, 0.6–0.7 mm wide, apex apiculate, with a minute appendage *c.* 0.05 mm long, pink to purplish to brown, margins white adaxially, median band darker. *Petals* narrowly oblong, 1.5–1.6 mm long, 0.5–0.6 mm wide, acute, white to cream, median band darker abaxially. *Filaments* held erect, straight or slightly incurving, subequal, 0.6–0.7 mm long, slightly dilated, minutely papillose, white; anthers *c.* 0.25 mm long. *Style* filiform, to 0.7 mm long, *c.* equal to stamens. *Capsule* spreading to pendulous, obpyriform, 2.0–2.6 mm long, 1.1–1.5 mm wide, brown, slightly wrinkled. *Seed* 1 per fruit, 1.9–2.4 mm long, *c.* 1.6 mm wide, glossy black to iridescent, longitudinally striate; caruncle conical distally, the lobes fused (Figure 6).

Diagnostic characters: Inflorescence branches stiff; racemules with 0 or 1 nodes, ±stiffly straight or sometimes diverging, pungent, 4–27 mm long, ribbed to narrowly winged, very finely covered in blunt, scabrid hairs 0.05–0.15 mm long.

Fig. 6. *Corynotheca acanthoclada*. A. Habit. B–D. Flowering branchlets. E. Lateral view of flower and buds. F. Flower and buds. Vouchers: Kalbarri, *J. Jackson & R. Simkin s.n.* (PERTH, A–D); Kalbarri, *R. Simkin s.n.* (PERTH, E, F). Photographs by J. Jackson (A–D); R. Simkin (E, F).

Other specimens examined: WESTERN AUSTRALIA: [Precise localities withheld for conservation reasons] Kalbarri, 30 Dec. 1988, *D. & B. Bellairs 2130* (PERTH); Kalbarri National Park, 10 Oct. 2019, *J. Jackson & R. Simkin s.n.* (PERTH); Greenough River, Oct. 1877, *F. Mueller s.n.* (MEL 107027, MEL 107028); Greenough River, Nov. 1877, *F. Mueller s.n.* (MEL 107031, MEL 107032); Greenough Back Flats, 20 Aug. 1998, *M.H. O'Connor MOC 0193* (PERTH); near West Binnu, 5 Oct. 2019, *R. Simkin s.n.* (PERTH); near Yandanooka, Nov. 1998, *R. Soullier 632* (PERTH).

Distribution: Restricted to near-coastal areas near Kalbarri, along the Murchison River, West Binnu, Yandanooka, and the Greenough Flats in Western Australia (Fig. 7).

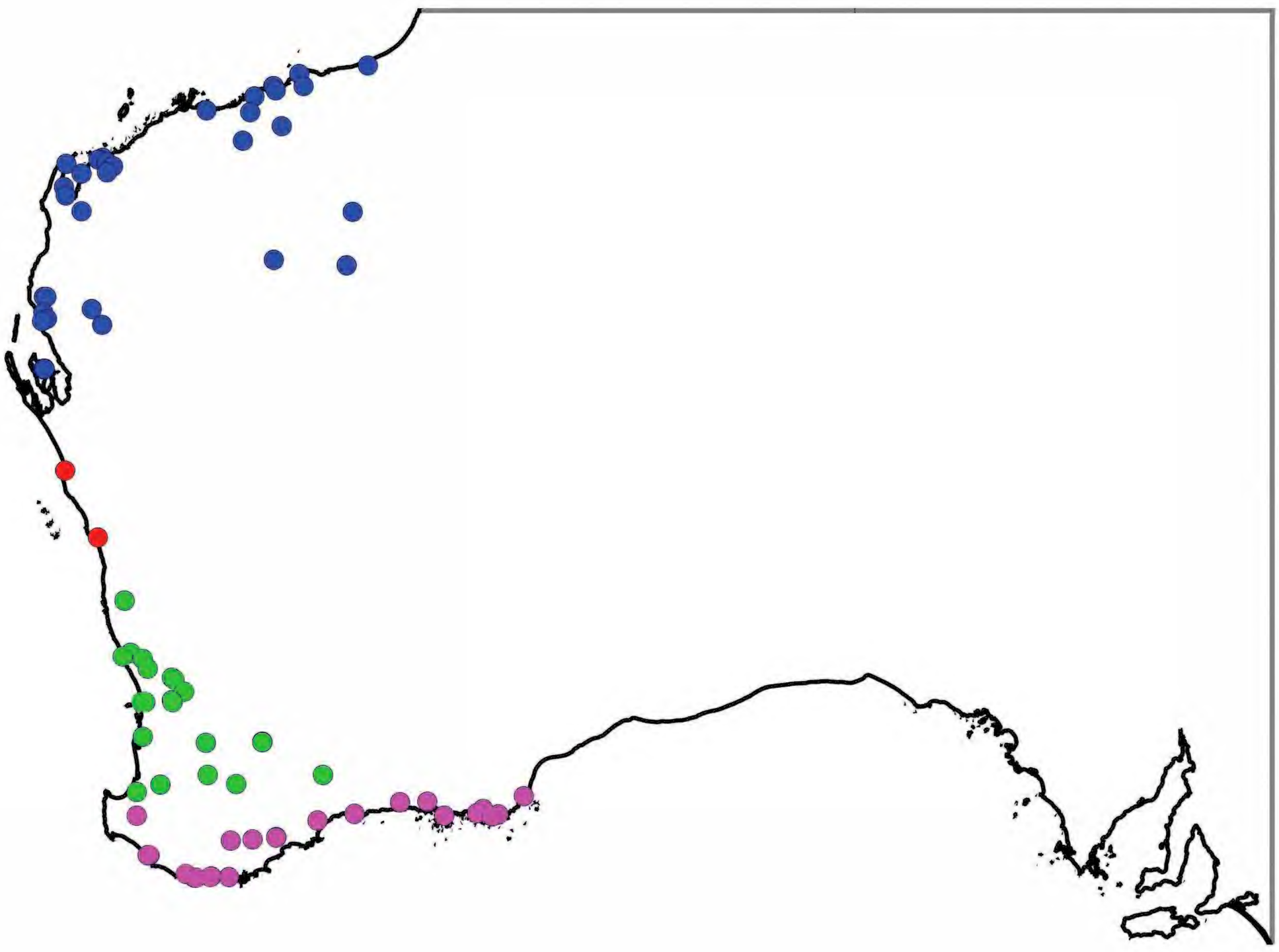

Fig. 7. Distribution map for *Corynotheca* species. *C. acanthoclada* (red); *C. elongata* (green); *C. panda* (pink); *C. pungens* (blue).

Habitat: Grows in sand over limestone, and white, yellow, brown or grey sandy alluvial loam over sandstone, in very open, low heath with scattered taller shrubs or open to closed shrubland. Most commonly seen post-fire or in areas that have been disturbed, such as roadsides, 1–4 years post-disturbance. Recorded in association with *Acacia acuminata*, *A. scirpifolia*, *Adenanthos cygnorum*, *Allocasuarina campestris*, *Banksia attenuata*, *Callitris arenaria*, *Chamelaucium marchantii*, *Cyphanthera racemosa*, *Cryptandra* sp., *Darwinia pauciflora*, *Daviesia pedunculata*, *Eucalyptus eudesmioides*, *Grevillea leucopteris*, *G. trifurcata*, *Gyrostemon racemiger*, *Lepidobolus* sp., *Melaleuca megacephala*, *Nuytsia floribunda*, *Pimelea angustifolia*, *Scaevola canescens*, *Schoenus* sp., *Scholtzia* spp. and *Stirlingia latifolia*.

Phenology: Flowers recorded for October–December.

Conservation status: *Corynotheca acanthoclada* is highly localised and it remains poorly collected. One population was recorded as 'frequent along roadside for *c.* 200 m', with a second, small population 400 m away. Another population observed in 2016 could not be relocated in 2018 due to localised disturbance. Several populations are known within Kalbarri National Park. To be listed as Conservation Priority 3 for Western Australian Flora (A. Jones, pers. comm.).

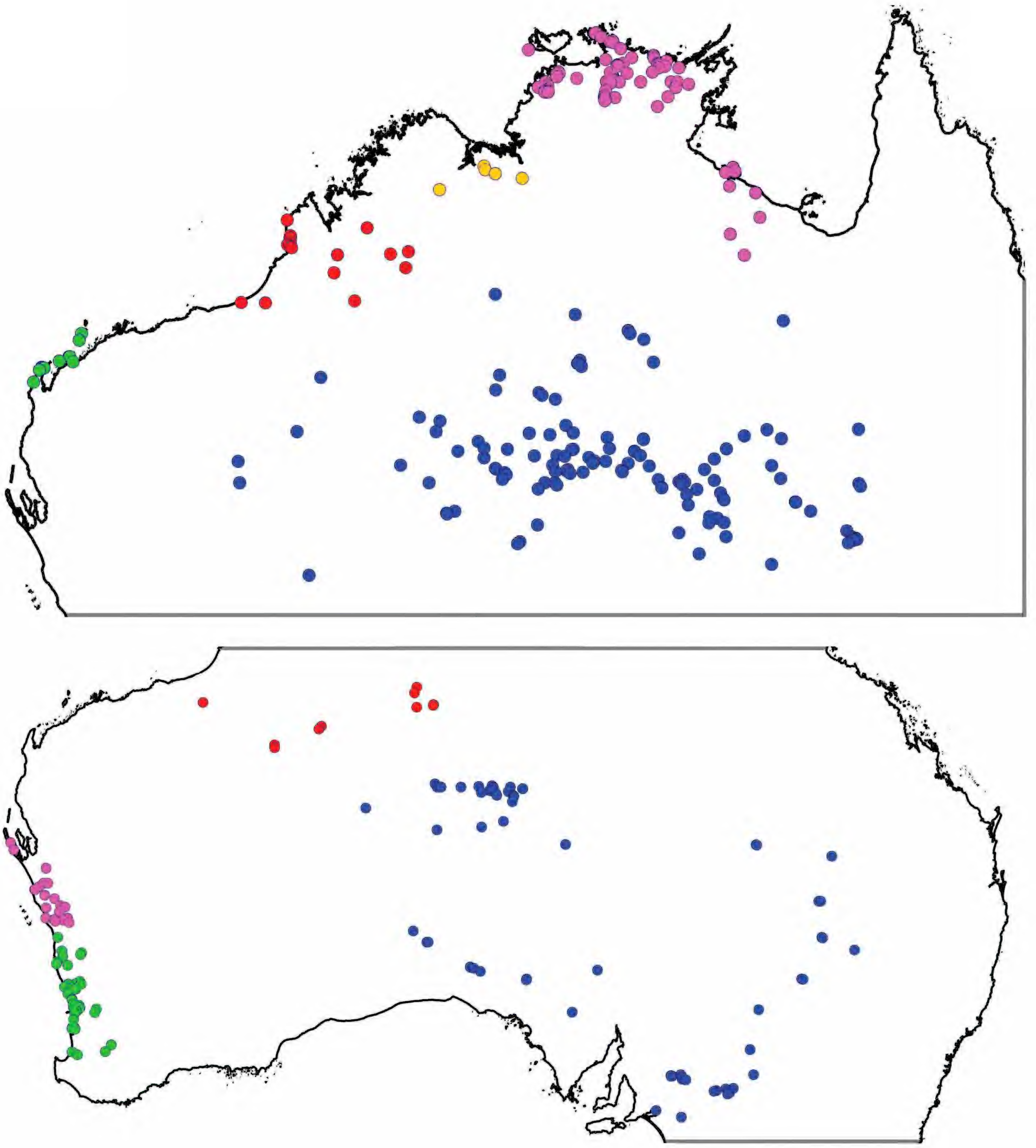

Fig. 8. Distribution maps for *Corynotheca* species. Map A (top): *C. borealis* (orange); *C. divaricata* (blue); *C. gracilis* (red); *C. flexuosissima* (green); *C. lateriflora* (pink). Map B (bottom): *C. asperata* (red); *C. dichotoma* (pink); *C. licrota* (blue); *C. micrantha* (green).

Common name: Spiny Zigzag Lily.

Etymology: The specific epithet is from the Greek *acantho-* (spiny) and *-cladus* (branch, shoot) in reference to the pungent racemule apices.

Affinities: *Corynotheca acanthoclada* may be related to *C. micrantha* and *C. elongata*, most readily distinguished from both species by the relatively short racemules that are rigid with pungent apices.

Notes: While Mueller (1870: 68) suggested this species might be best placed in a separate genus '*Corynotheca*', the combination was only validated by Bentham (1878: 50) who also validated the genus.

Henderson (1987: 474) designated material at MEL as the lectotype, but as two sheets are present at MEL, a second step lectotype is designated here to select a single sheet.

As a disturbance opportunist, this species may be relatively short-lived (R.Simkin, pers. comm.). It is also possible that it is longer-lived, but quickly overgrown and difficult to find once surrounding vegetation has recovered from the disturbance event.

Corynotheca asperata R.J.F.Hend., *Fl. Austral.* 45: 473, 304, fig. 96j (1987).

Type: *c.* 18 miles [*c.* 29 km] S of Inningarra Range, Northern Territory, 3 August 1970, *J.R. Maconochie 939* (holo: BRI AQ0053440; iso: NT A0027837*).

Tufted, tangled, rhizomatous *perennial*, upper parts scabrous. *Roots* not seen. *Stems* not seen. *Leaves* few, linear-subulate, to 30 mm long, flat, reducing rapidly to bracts upwards, all usually senesced by anthesis. *Inflorescence* perennating, irregularly paniculate, to 60 cm long, dark green; peduncle ascending to decumbent, subterranean at base; major branches spreading to decumbent; lowest branch 1–3 cm from rhizome; branching at 80–100°; panicle branches flexuose, each node diverging at 140–170°; racemules with axis tortuous, 4–23(–50) mm long, with (0)1–6 nodes, each node divaricate at 140–180°, but sometimes reduced to 1 internode 4–8 mm long, finely ribbed, scabrid; internodes 2–11 mm long, 0.5–0.7 mm wide, ±straight; flowers solitary (?or rarely paired) in branch axils, ?few developing; lower bracts linear, ±pungent, 5–20 mm long, acuminate; uppermost bracts minute, needle-shaped, 3–4 mm long; pedicels 0.3–0.8 mm long. *Perianth* 4.5–6.3 mm long, segments connate for *c.* 0.5 mm, spirally twisting after anthesis, deciduous. *Sepals* narrowly elliptic to oblong, 4.6–6.2 mm long, 0.9–1.1 mm wide, apex apiculate, with a minute appendage *c.* 0.5 mm long, pink to purplish to brown, median band darker. *Petals* narrowly elliptic, 4.5–6.1 mm long, 0.8–1.0 mm wide, obtuse, white to cream, median band darker. *Filaments* not examined; anthers 0.8–1.0 mm long. *Style* not examined. *Capsule* not seen (Figure 9).

Fig. 9. *Corynotheca asperata*. A. Habit. B. Inflorescence with closed flowers. Voucher: Tanami Downs Station, *D.E. Albrecht 12673* (NT). Photographs by D.E. Albrecht.

Diagnostic characters: Inflorescence axes and racemules finely scabrid; pedicels 0.3–0.8 mm long.

Other specimens examined: WESTERN AUSTRALIA: [precise localities withheld for conservation reasons] North Pilbara, July 2014, *S. Colwill* & *M. Henson WB 37311* (PERTH); East Pilbara, May 1979, *A.S. George*

15589 (DNA, *n.v.*, PERTH); East Pilbara, May 1979, *A.S. Mitchell 1065* (DNA, *n.v.*, PERTH); NORTHERN TERRITORY: *c.* 1.5 km S of Wild Potato Bore, Tanami Downs Station, 17 July 2008, *D. Albrecht 12673* (DNA, *n.v.*, NT); 8 km S of Sangsters Bore, Tanami Desert, 8 Aug. 1982, *P.K. Latz 9388* (AD, DNA, *n.v.*).

Distribution: Only known from a few collections along the southern margins of the Great Sandy Desert in Western Australia, and from the adjacent Tanami Desert in the Northern Territory (Figure 8B).

Habitat: Grows on red sand dunes with *Acacia torulosa*, *Aristida holathera*, *Chamaecrista symonii*, *Crotalaria cunninghamii*, *Dicrastylis doranii*, *Triodia epactia* and *T. schinzii*.

Phenology: Flowers mostly from May–August.

Conservation status: *Corynotheca asperata* is listed as Priority Three under conservation codes for Western Australian flora. Listed as Data Deficient in the Northern Territory.

Common name: Rough Zigzag Lily.

Etymology: The specific epithet is from the Latin *asperatus* (rough with points or sharp stiff hairs), in reference to the sparse, even indumentum of short, stiff, erect hairs on the inflorescence axes.

Affinities: *Corynotheca asperata* may be most closely related to *C. divaricata*, sharing a robust habit and arid habitats, differing in the scabrous (*vs* glabrous) inflorescence axes, racemules with (0)1–6 (*vs* 5–8(–10)) nodes and 4–23(–50) (*vs* 17–95) mm long.

Notes: Henderson (1987) did not see any material with fruit or seeds and they remain uncollected.

Corynotheca borealis R.L.Barrett, Keighery & T.Macfarlane, *sp. nov*.

Type: Keep River National Park, SW of Jarrnarm, Northern Territory, 19 June 1995, *J.L. Egan* 5107 (holo: CANB 00531761.1, CANB 00531761.2 [a single specimen mounted on two sheets]; iso: DNA D0123729*).

Tufted, tangled, rhizomatous *perennial*, glabrous. *Roots* not seen. *Stems* not seen. *Leaves* few, linear-subulate, 6–25 mm long, 0.4–0.7 mm wide, flat, reducing rapidly to bracts upwards, all usually senesced by anthesis. *Inflorescence* perennating, irregularly paniculate, 45–90 cm long, dark green; peduncle ascending to spreading, subterranean at base; major branches mostly erect; lowest branch 6–20 cm from rhizome; panicle branches dichotomously divaricate, each node divaricate at 90–160°; racemules with axis not or slightly tortuous, 10–75 mm long, with 1–5 nodes, each node divaricate at 80–100°, finely ribbed, but otherwise smooth; internodes 5–11 mm long, 0.2–0.4 mm wide, ±straight; flowers solitary, most developing, subtended by a small bract; lower bracts ±narrowly triangular, 4–8 mm long, acuminate; uppermost bracts ±triangular, 0.4–0.5 mm long; pedicels 0.9–1.3 mm long (elongating to 2.4 mm long in fruit). *Perianth* 3.9–5.0 mm long, segments connate for 0.6–0.7 mm, spirally twisting after anthesis, deciduous. *Sepals* narrowly elliptic to narrowly oblong-elliptic, 4.2–4.5 mm long, 0.8–0.9 mm wide, apex apiculate, with a minute appendage *c.* 0.3 mm long, cream to brown, median band brown. *Petals* narrowly oblong to narrowly elliptic, 4.1–4.5 mm long, 0.7–0.8 mm wide, obtuse, white to cream, median band darker. *Filaments* slightly spreading, straight or slightly incurving, 1.4–2.1 mm long, unequal, dilated and minutely papillose in lower half, yellow; anthers *c.* 0.5 mm long. *Style* filiform, to *c.* 1.8 mm long, not exceeding stamens. *Capsule* antrorse, fusiform to obpyriform to obovate, 4.1–5.2 mm long, 1.8–2.3 mm wide, brown, slightly wrinkled. *Seed* 1 per fruit, 3.8–4.2 mm long, *c.* 2.0 mm wide, glossy black to brown, longitudinally striate; caruncle conical distally, blackish, the lobes fused (Figure 10).

Diagnostic characters: Racemule internodes diverging at 80–100°; pedicels 0.9–1.3 mm long; staminal filaments 1.4–2.1 mm long.

Other specimens examined: WESTERN AUSTRALIA: Carlton Road, NW, KRS [Kimberley Research Station], Kununurra, 7 Dec. 1978, *M.H. Andrew 177* (BRI, CANB, DNA, *n.v.*); 9 mi. E of Kimberley Research Station, 23 July 1949, *R.A. Perry 2571* (AD, *n.v.*, BRI, NSW, PERTH); Karunji Station, 7 Mar. 1950, *D.W. Rust 88* (CANB, PERTH). NORTHERN TERRITORY: Auvergne Station, 13 Mar. 1998, *R. Harwood 450 & P. Brocklehurst* (DNA).

Distribution: Of restricted distribution near Kununurra, extending south to Karunji Station in Western Australia and from Keep River National Park east to Pelican Creek (Auvergne Station) in the Northern Territory (Figure 8A).

Habitat: Grows on red 'cockatoo' sand flats in open woodland below sandstone. Associated species include *Acacia tumida* and *Corymbia polycarpa*.

Phenology: Flowers between December and June. Fruit recorded in Sept.

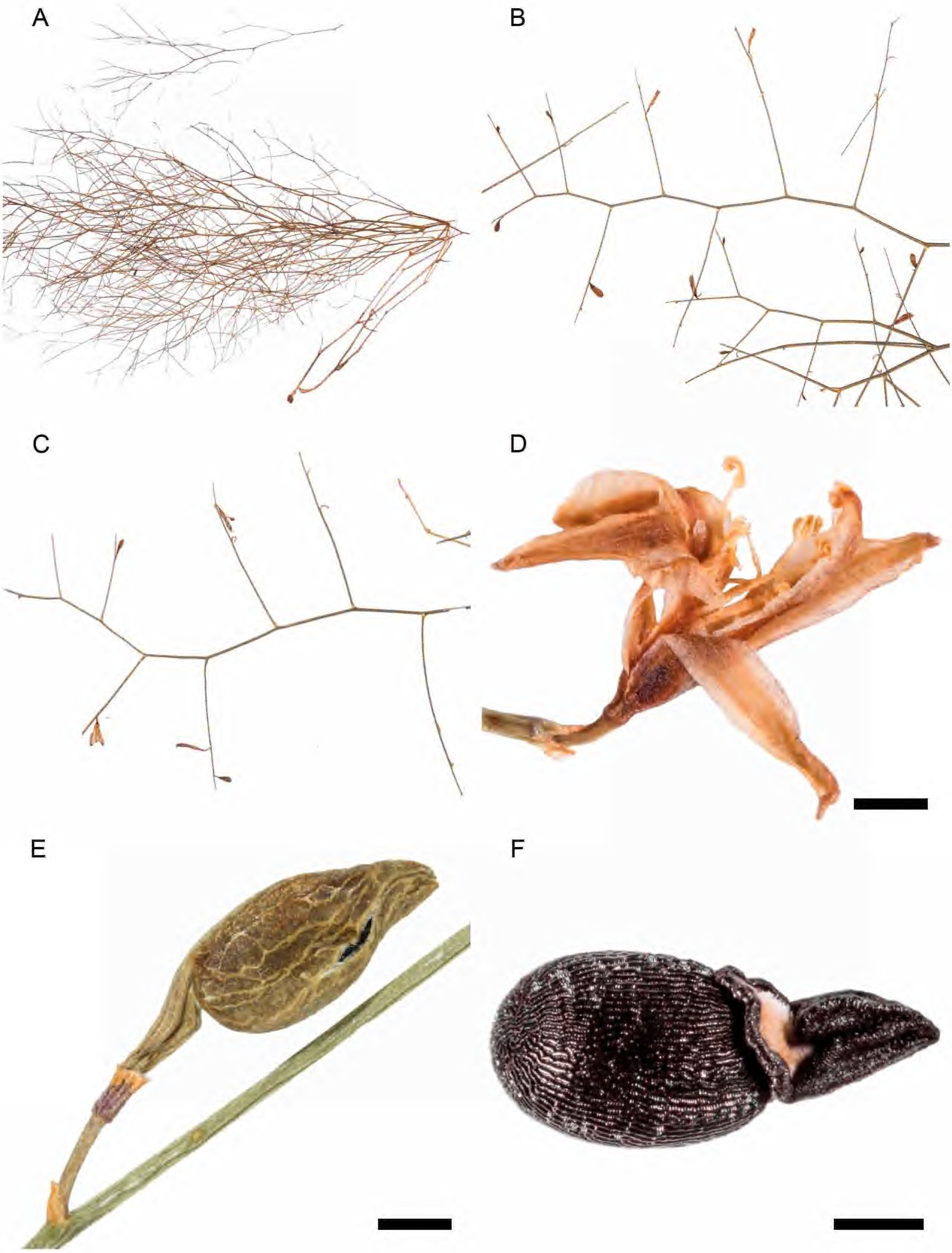

Fig. 10. *Corynotheca borealis*. A. Habit. B, C. Flowering branches. D. Flower. E. Fruit. F. Seed. Vouchers: A: Karunji Station, *D.W. Rust 88* (CANB); B–F: Keep River National Park, *J.L. Egan 5107* (CANB). Scale = 1 mm. Photographs by R.L. Barrett.

Conservation status: *Corynotheca borealis* is poorly known and should be listed as a Priority 1 taxon in Western Australia and Data Deficient in the Northern Territory. Searches for this species in the vicinity of the Kimberley Resaerch Station in January 2021 failed to locate any populations (M.D. Barrett, pers. comm.), but the original collection locations are each somewhat unclear and populations may yet be extant in the area.

Common name: Northern Zigzag Lily.

Etymology: The specific epithet refers to the northern distribution in relation to its closest relative, *C. gracilis*.

Affinities: *Corynotheca borealis* is most closely related to *C. gracilis*, differing in the racemule internodes diverging at 80–100° (*vs* 110–140°); pedicels 0.9–1.3 mm long (*vs* 1.0–3.1 mm long); sepals 0.8–0.9 mm wide (*vs* 1.1–1.4 mm wide), petals 0.7–0.8 mm wide (*vs* 1.4–1.5 mm wide) and staminal filaments 1.4–2.1 mm long (*vs* 1.9–4.0 mm long).

Notes: This taxon has previously been confused with *C. lateriflora*. *Corynotheca borealis* can be readily distinguished from *C. lateriflora* by the racemules with axis not or slightly tortuous (*vs* tortuous), 10–75 mm long (*vs* 65–175(–250) mm long), with 1–5 nodes (*vs* 4–7), each node divaricate at 80–100° (*vs* diverging at 170–180°) and internodes 5–11 mm long (*vs* 7–31(–40) mm long). All previous records of *C. lateriflora* from Western Australia represent either *C. borealis* or *Tricoryne* sp. Kimberley (K.F. Kenneally 4857).

Corynotheca dichotoma (F.Muell.) F.Muell. ex Benth., *Fl. Austral.* 7: 50 (1878); *Caesia dichotoma* F.Muell., *Fragm.* 1(9): 215 (1859).

Type: Mouth of the Murchison R., Western Australia, *n.d.*, *A.F. Oldfield s.n.* (lecto: MEL 107033), designated by R.J.F.Henderson, *Fl. Austral.* 45: 301 (1987), (as 'holo'); N. [presumably Mouth] of the Murchison R., W.A., *A.F. Oldfield s.n.* (presumed isolecto: MEL 107035).

Tufted, tangled, rhizomatous *perennial*, glabrous. *Roots* many, 150–250 mm long, fleshy-fibrous, sand-binding. *Stems* short, to 35 mm long and 7 mm wide. *Leaves* few, linear-subulate, to 67 mm long, 0.8–1.5 mm wide, flat, reducing rapidly to bracts upwards, all usually senesced by anthesis. *Inflorescence* perennating, irregularly paniculate, to 105 cm long, dark green; peduncle ascending to decumbent, subterranean at base; major branches decumbent; lowest branch 7–34 cm from rhizome; panicle branches dichotomously divaricate, each node divaricate at 80–140°; racemules with axis tortuous, 15–60 mm long, with (1–)5–13 nodes, each node divaricate at 80–110°, but sometimes reduced to 1 internode *c.* 1.5 mm long, finely ribbed, but otherwise smooth; internodes 1–7 mm long, (0.2–)0.4–0.6 mm wide, ±straight; flowers solitary in branch axils, ?most developing; lower bracts linear-subulate, 7–17 mm long, acuminate; uppermost bracts obovate to ±triangular, 0.6–1.2 mm long; pedicels 0.8–2.3 mm long. *Perianth* 4.1–5.0 mm long, segments connate for *c.* 0.5 mm, spirally twisting after anthesis, deciduous. *Sepals* narrowly oblong, 2.9–4.5 mm long, 0.8–1.1 mm wide, apex apiculate, with a minute appendage *c.* 0.2 mm long, mostly white, median band grading to pink to purplish to brown, margins white. *Petals* narrowly oblong, 4.6–4.8 mm long, 0.9–1.0 mm wide, acute, white to cream, median band sometimes darker abaxially. *Filaments* widely spreading, straight or slightly incurving, 2.2–2.7 mm long, subequal, not or only slightly dilated, minutely papillose, white; anthers 0.7–0.9 mm long. *Style* filiform, to 3.7 mm long, exceeding stamens. *Capsule* antrorse, obpyriform, 2.9–3.4 mm long, *c.* 1.8 mm wide, brown, slightly wrinkled. *Seed* 1 per fruit, 2.9–3.3 mm long, *c.* 1.5 mm wide, glossy black to iridescent, longitudinally striate; caruncle conical distally, the lobes fused. *2n* = 42 (G.J. Keighery, *Feddes Repert.* 95: 527 (1984); *Keighery 1789*, as *C.* '*macrantha*') (Figures 5b, 11).

Diagnostic characters: Racemule 15–60 mm long, with (1–)5–13 internodes, diverging at 80–110°, internodes 1–7 mm long, inflorescence dense, but not gnarled and perianth 4.1–5.0 mm long.

Other specimens examined: WESTERN AUSTRALIA: NW Coastal Highway, *c.* 42 km by road N of Murchison River crossing, 2 Sept. 1977, *W.R. Barker 2191* (AD, MEL, NSW); 9.3 km S on Moore Road from Geraldton–Mt Magnet Road, on E side of road, Indarra Nature Reserve, Western Australia, 20 Oct. 2008, *R.L. Barrett & B.G. Briggs RLB 5280* (CANB, K, MEL, NSW, PERTH); 13 miles W of Kalbarri turnoff from NW Coastal Highway, 5 miles NW of Mount View, S of Murchison River, 22 Aug. 1965, *A.C. Beauglehole ACB 11926* (PERTH); Emu Springs in Kalbarri National Park, 25 Nov. 1995, *D.* & *B. Bellairs 3010* (CANB); Balla, 13 Oct. 1964, *W.H. Butler s.n.* (PERTH); Wandana Reserve, 9 Oct. 2006, *G. Byrne 2430* (PERTH); 411 mile peg on Geraldton – Carnarvon road [6 km N of Billabong Roadhouse on North West Coastal Highway], 18 Mar. 1958, *S.G.M. Carr 444* (PERTH); S end Moore Road junction Eves Road, 25 Nov. 2001, *J. Docherty 82* (PERTH); Near Homestead, Dirk Hartog Island, 3 Sept. 1972, *A.S. George 11416* (PERTH); upper Irwin River, *J. Guerin s.n.* (MEL 107053); *c.* 12 km S of Billabong Roadhouse, 6 Aug. 1976, *R. Hnatiuk 760405* (PERTH); 10.5 km E of Kalbarri town, 19 Sept. 1974, *G.J. Keighery 1789* (PERTH); 8 km S along Indarra South Road, from Geraldton to Mullewa Road, 20 km S of Mullewa, 25 Oct. 1988, *G.J. Keighery 10922* (PERTH); Upper Irwin River, Nov. 1877, *O.L. Jones s.n.* (MEL 107045, MEL 107046, MEL 107047); *c.* 3 km SW of Trig Station Spit, Heirisson Prong, Shark Bay, West of Rubberneck Road, 26 Sept. 1997, *A. Markey 1478* (PERTH); Greenough River, Nov. 1877, *F.Mueller s.n.* (MEL 107040); lower Greenough River, Nov. 1877, *F.Mueller s.n.* (MEL 107041); E margin of Kalbarri National Park, 26 Nov. 1974, *R. Pullen 9647* (BRI, CANB, HO, *n.v.*, NSW, PERTH); between the Murchison and Irwin Rivers, *Miss Sewell s.n.* (MEL 107042); Waggrakine, at base of Moresby Range, 27 Oct. 1998, *S. Vigilante 5* (PERTH); Yardanogo Nature Reserve (NR 36203), 8.3 km E of Brand Highway on Mt Adams Road, 4 Nov. 2008, *V. Westcott S.M. 75 A* (PERTH); Quadrat WEST 2 on Eurardy Station, *c.* 43 km N of Kalbarri turn-off on the North West Coastal Highway and N of Murchison River, 3 Oct. 2003, *Wildflower Society of WA EURA 258* (PERTH).

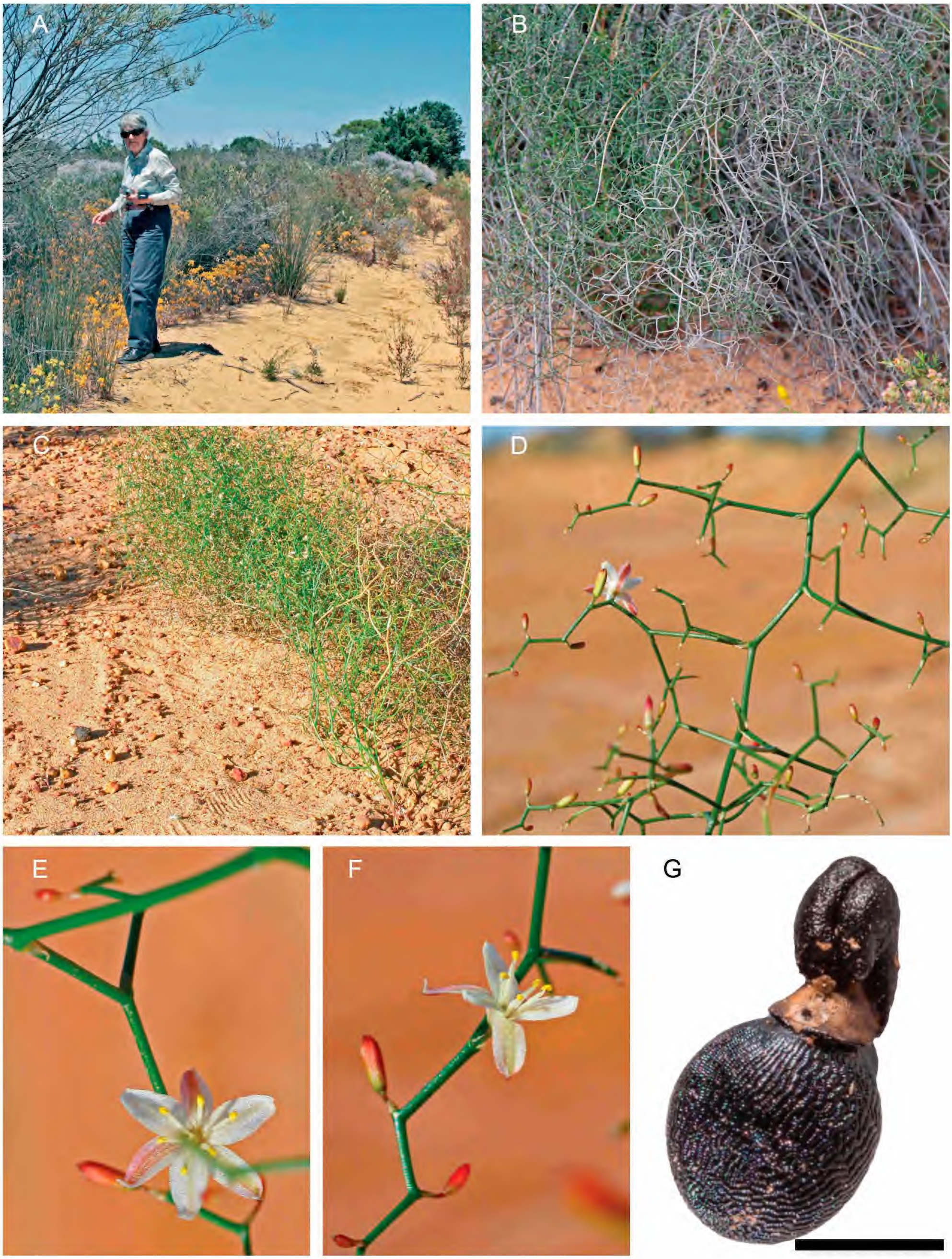

Fig. 11. *Corynotheca dichotoma*. A. Habitat with Barbara Briggs, 2008. B, C. Habit. D. Flowering branches. E, F. Flowering branchlet. G. Seed. Vouchers: East Yuna Nature Reserve (A, B); Wandana Nature Reserve, *G. Byrne 2430* (PERTH; C–F); and Indarra Nature Reserve, *R.L. Barrett & B.G. Briggs RLB 5280* (PERTH; G). Scale = 1 mm. Photographs by R.L. Barrett (A, B, G) G. Byrne (C–F).

Distribution: Scattered in the Mid West region of southern Western Australia, from near Mullewa, north to Shark Bay and Dirk Hartog Island (Figure 8B).

Habitat: Grows on yellow sand flats and sand dunes, on deep sands or over clay or laterite. Associated species include *Acacia scirpifolia, A. rostellifera, Anthotroche myoporoides*, *Baeckea robusta*, *Banksia prionotes, B. sceptrum*, *Calothamnus glaber*, *Calytrix brevifolia*, *C. strigosa*, *Comesperma griffinii*, *Conostylis resinosa*, *Ecdeiocolea monostachya*, *Enchylaena tomentosa*, *E. rigens*, *Eucalyptus gittinsii*, *Grevillea annulifera*, *G. bracteosa*, *G. leucopteris*, *Hakea bucculenta*, *Harperia ferruginipes*, *Jacksonia velutina*, *Lachnostachys eriobotrya*, *Lepidobolus basiflorus*, *L. densus*, *L. eurardyensis*, *L. preissianus* subsp. *volubilis*, *Mesomelaena pseudostygia*, *M. stygia*, *Persoonia acicularis*, *P. biglandulosa*, *Petrophile pilostyla* subsp. *syntoma*, *Pileanthus peduncularis*, *Schoenus pennisetis*, *S.* sp. Indarra (R.L. Barrett & B.G. Briggs RLB 5277), *Scholtzia* sp. Binnu (M.E. Trudgen 2218), *Thryptomene hubbardii*, *Verreauxia reinwardtii* and *Xylomelum angustifolium*.

Phenology: Flowers mostly between August and November, or later in response to summer rainfall events. Only a single collection, made in March, is in fruit, suggesting that ideal conditions may be required for fruit set. Flowers are noted to usually open in the late afternoon.

Conservation status: *Corynotheca dichotoma* is known to occur in several National Parks and Nature Reserves and is not currently considered threatened.

Common name: Intricate Zigzag Lily.

Etymology: The epithet is from the Latin *dichotomos* (dividing in half), in reference to the regular divergence of the stems of this species.

Affinities: *Corynotheca dichotoma* appears most similar to *C. flexuosissima* R.J.F.Hend. based on the compact inflorescence with smooth axes, but is also superficially similar to *C. asperata* R.J.F.Hend. in inflorescence branching pattern, but that species is very distinctive in having finely scabrid (*vs* glabrous) stems, fibrous (*vs* fleshy-fibrous) roots and racemules with (0)1–6 (*vs* (1–)5–13) nodes. *Corynotheca dichotoma* can be readily distinguished from *C. flexuosissima* by the more openly branching racemules 15–60 (*vs* 4–12(–25)) mm long, with (1–)5–13 (*vs* (5–)9–20) nodes, internodes 1–7 (*vs* 0.8–2) mm long, longer peduncles 0.8–2.3 (*vs* 0.2–0.9) mm long and larger perianth 4.1–5.0 (*vs* 1.4–2.1) mm long.

Notes: Henderson (1987) commented under his *C. micrantha* var. *micrantha* that "Field studies may show material included here represents more than one taxon" and one of the cited specimens (Pullen 9647) is here included under *C. dichotoma* following examination of this species in the field.

While Mueller (1870: 68) suggested that *Caesia dichotoma* might be best placed in *Corynotheca*, the combination was only validated by Bentham (1878: 50). Henderson (1987) designated a single collection at MEL as 'holo', however two collections are held at MEL, with differing label information, so Henderson's designation is here corrected to an effective lectotypification. The label of the second specimen has generally been interpreted as 'N.' [North], but is probably 'M.' [Mouth], in which case it is most likely a duplicate of the lectotype.

Corynotheca divaricata (R.J.F.Hend.) R.L.Barrett & T.Macfarlane, *comb. et. stat. nov.*

Basionym: *Corynotheca micrantha* var. *divaricata* R.J.F.Hend., *Fl. Austral.* 45: 474, 303, fig. 70i (1987).

Type: Cordillo Downs, *c.* 40 km W and *c.* 8 km S of Qld border, South Australia, 19 October 1963, *anon. ex Pastoral Board s.n.* (holo: AD 97916036*).

Corynotheca lateriflora auct. non (R.Br.) F.Muell. ex Benth.: Jessop, J.P. in Jessop, J.P. & Toelken, H.R. (ed.) *Fl. S. Austral.* Edn. 4, 4: 1752 (1986), *p.p.*

Tufted, tangled, rhizomatous *perennial*, glabrous. *Roots* many, 50–180 mm long, fleshy-fibrous, sand-binding. *Stems* short, to 20 mm long and 5 mm wide. *Leaves* few, linear-subulate, 14–68 mm long, 1.6–2.9 mm wide, flat, reducing rapidly to bracts upwards, all usually senesced by anthesis. *Inflorescence* perennating, uninterrupted, evenly diffuse, irregularly paniculate, to 60(–80) cm long, dark green; peduncle ascending to decumbent, subterranean at base; major branches spreading to decumbent; lowest branch 9–29 cm from rhizome; panicle branches dichotomously divaricate, each node divaricate at 90–140°; racemules with axis tortuous, 17–95(–180) mm long, with 5–8(–10) nodes, each node diverging at 140–180°, finely ribbed, but otherwise smooth; internodes 4–13 mm long, ±straight, 0.4–0.9 mm wide; flowers solitary or commonly paired (sometimes in threes) in branch axils, most developing; lower bracts linear-subulate, 6–38 mm long, acuminate; uppermost bracts obovate to ±triangular or subulate, 1.2–7.1 mm long; pedicels 0.3–1.2(–2) mm long. *Perianth* 4.1–5.9 mm long, segments connate for *c.* 0.8 mm, spirally twisting after anthesis, deciduous. *Sepals* narrowly oblong, 2.9–5.1 mm long, 0.8–1.0 mm wide, apex apiculate, with a minute appendage *c.* 0.5 mm long, brown abaxially, margins white to mauve to pink adaxially, median band brown adaxially. *Petals* narrowly oblong, 2.8–5.0 mm long, 0.7–1.1 mm wide, acute, white to cream to mauve, median band brown. *Filaments* slightly spreading, often kinked at the base, sometimes straight or slightly incurving, 1.4–1.8 mm long, unequal, dilated and minutely papillose, yellow; anthers 0.6–0.7 mm long. *Style* filiform, to 1.7 mm

long, shortly exceeding stamens. *Capsule* erect to pendulous, obpyriform, 4.9–7.2 mm long, 1.3–1.9 mm wide, brown, slightly wrinkled. *Seeds* 1 or 2(3) per fruit, 2.3–3.7 mm long, 1.2–1.5 mm wide, very glossy black to iridescent, smooth to very finely pitted; caruncle conical distally, the lobes fused. *2n* = 42 (G.J. Keighery, *Feddes Repert*. 95: 527 (1984); *Keighery 563*, as *C. lateriflora*) (Figures 2, 12).

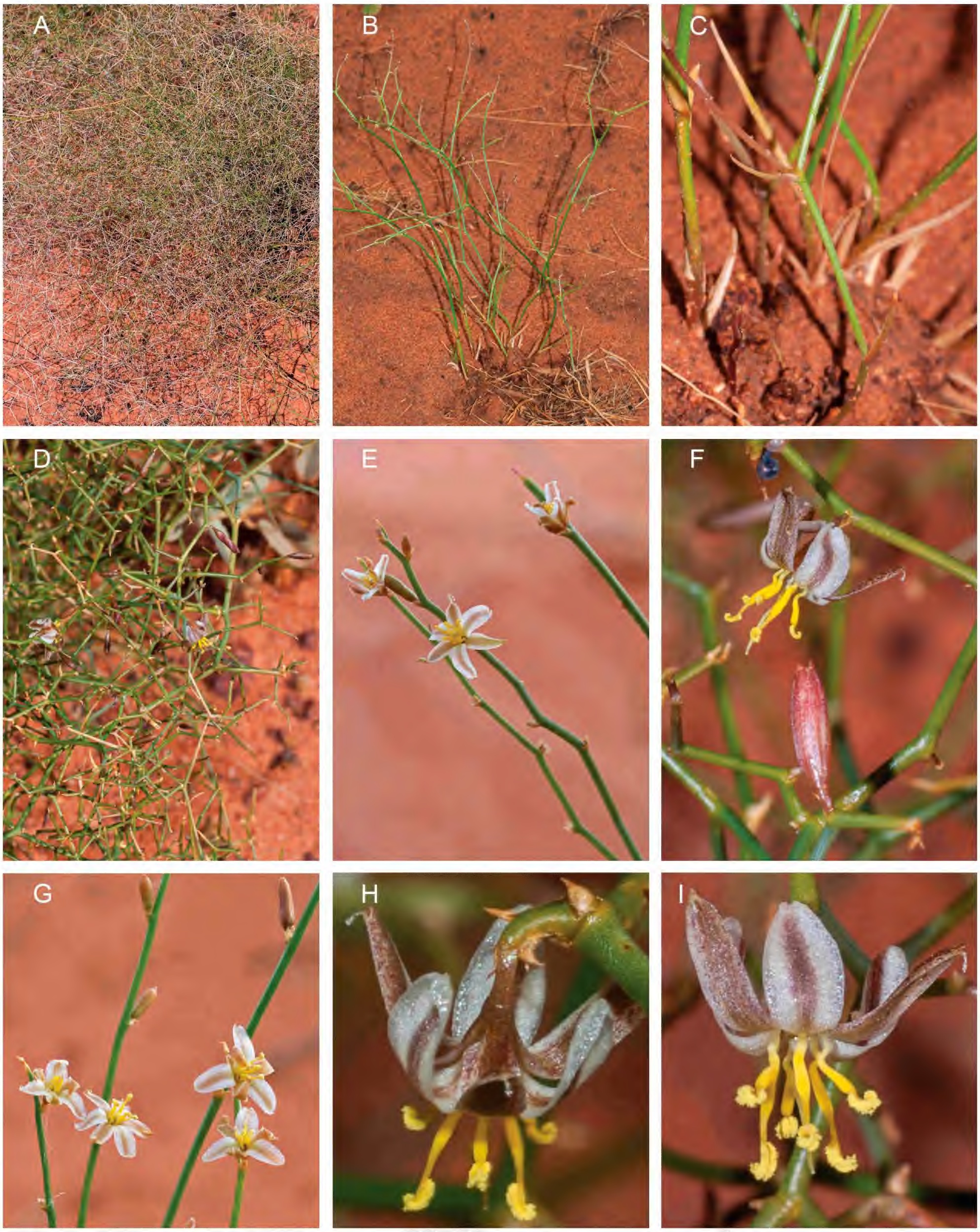

Fig. 12. *Corynotheca divaricata*. A. Habit. B. Plant resprouting after fire. C. Plant base. D. Flowering branches. E. Racemules. F. Flower and developing fruit. G, H. Flowers. I. Seed. Vouchers: A, D, F, G: Shay Gap, *R.L. Barrett RLB 8238* (PERTH); B, C: Browns Range, WA (not vouchered); E: near Kuta Juta, *D.E. Albrecht 12942* (NT) and F: Waite Creek, *N. Henry 365* (NSW). Scale = 1 mm. Photographs by R.L. Barrett (A–D, F–I) and D.E. Albrecht (E).

Diagnostic characters: Basal leaves 1.6–2.9 mm wide, racemules 17–95(–180) mm long, with 5–8(–10) nodes, internodes 4–13 mm long, pedicels 0.3–1.2 mm long, perianth 4.1–5.9 mm long, seed testa smooth to very finely pitted.

Selected specimens examined: WESTERN AUSTRALIA: 1.4 km S on Boreline Road from Great Northern Highway, E of Pardoo Roadhouse, Dampier Botanical District, 26 July 2013, *R.L. Barrett RLB 8238* (PERTH); Gibson Desert, Gibber Plains area, 90 km SW of Lake Christopher, 9 May 1980, *J.M. Bechervaise & J. Kelso 7* (MEL); 50 miles NE of Cosmo Newberry Mission, 28 Sept. 1966, *A.S.George 8116* (PERTH); beyond the Alfred Maries Range, *W.E.P. Giles s.n.* (MEL 107038); near Sally May well site, Great Sandy Desert, 28 June 2009, *G.F. Griffin & S.R. Dunlop GSD 09-117* (PERTH); Barrow Range, 19 Aug. 1891, *R. Helms s.n.* (MEL 107039); Little Sandy Desert, northern edge of Lake Sunshine, 19 Aug. 2001, *S. van Leeuwen 4993* (AD, *n.v.*, CANB, PERTH). NORTHERN TERRITORY: 20 km NNW of Finke Settlement, 10 Nov. 1993, *D.E. Albrecht 5640* (BRI, DNA, *n.v.*, MEL, NSW, NT, *n.v.*); *c.* 17 km NW of Mt Campbell, 6 May 1958, *G. Chippendale 4312* (AD, *n.v.*, BRI, CANB, DNA, *n.v.*, MEL, NSW, PERTH); SE corner of Lake Amadeus, Central Australia, 29 June 1959, *G. Chippendale 6369* (AD, *n.v.*, CANB, DNA, *n.v.*, MEL, NSW, PERTH); Lake Mackay, on island on SE edge of lake, 10 Oct. 1992, *P.K. Latz 12868* (DNA, *n.v.*, K, *n.v.*, MEL, MO, *n.v.*, NSW, NT, *n.v.*), South Tobermorey Station, Simpson Desert, 25 Oct. 2001, *P.K. Latz 18195* (BRI, NT, *n.v.*); Uluru (Ayers Rock - Mt Olga) National Park: on the Docker River Road, 17 May 1988, *M. Lazarides & J. Palmer 179* (AD, *n.v.*, CANB, DNA, *n.v.*). SOUTH AUSTRALIA: Mokari, Simpson, 27 Aug. 1977, *R. Buckley 1712 (ANU 26612)* (CANB); *c.* 7 km ESE of Marqualpie Waterhole, 12 May 1987, *R.W. Purdie 2923A* (AD, *n.v.*, CBG); Far North, in from W edge of Simpson Desert, 78.4 km, via Purnie and Mokari Bores, 28 Sept. 1974, *D.E. Symon 9443* (AD, *n.v.*, CANB, DNA, *n.v.*). QUEENSLAND: 37 km SE of Springvale, 30 Sept. 1982, *R.J. Chinnock 5567* (AD, CBG); SW corner of Pilpah Range, 12.5 km NNE of Barkly Downs homestead, 10 Nov. 2004, *D.T. Kelman DTK 101104-9 & C. Kahler* (BRI); Warlus VI, Site R56 (24 km SE of Betoota), 18 Sept. 1977, *R.W. Purdie 1144* (BRI); 8 km S of Mooraberrie Station, 6 Nov. 1978, *R.W. Purdie 1151* (CBG); Farriers Creek, Morney Plains Station, 9 Sept. 2011, *D. Richter DR 271 & G.P. Turpin* (BRI).

Distribution: A widespread species in inland Australia, from near Wiluna north to Shay Gap and the Tanami Desert in Western Australia, through central Northern Territory and the north of South Australia to Springvale in south east Queensland (Figure 8A).

Habitat: Grows on sand dunes and sandy ridges in low, open shrubland with *Acacia hilliana*, *A. monticola*, *A. tumida*, *Allocasuarina decaisneana*, *Aristida holathera*, *Calandrinia eremaea*, *Corymbia zygophylla*, *Crotalaria cunninghamii*, *C. eremaea*, *Eragrostis basedowii*, *Goodenia scaevolina*, *Grevillea juncifolia*, *G. stenobotrya*, *Gyrostemon ramulosus*, *Halgania solanacea*, *Heliotropium transforme*, *Lechenaultia divaricata*, *Newcastelia cladotricha*, *Polymeria lanata*, *Ptilotus axillaris*, *P. incanus*, *Solanum centrale*, *S. diversiflorum*, *S. phlomoides*, *Trachymene oleracea*, *Triodia basedowii, T. pungens* and *Zygochloa paradoxa*.

Phenology: Flowers mainly (July–)August–December, but also recorded for March–April.

Conservation status: *Corynotheca divaricata* is widespread and is not currently considered threatened.

Common names: Desert Zigzag Lily, Sand Lily.

Etymology: The specific epithet is from the Latin *divaricatus* (widely spreading), in reference to the divaricate, ±straight racemules and inflorescence axes.

Affinities: *Corynotheca divaricata* may be most closely related to *C. asperata*, sharing a robust habit and arid habitats, differing in the glabrous (*vs* scabrous) inflorescence axes, racemules with 5–8(–10) (*vs* (0)1–6) nodes, 17–95 (*vs* 4–23(–50)) mm long. Sometimes confused with *C. licrota* which has an erect (*vs* spreading) habit, fibrous (*vs* fleshy-fibrous) roots, persistent (*vs* dry at anthesis) leaves 50–300(–600) (*vs* 14–68) mm longand striate (*vs* smooth to finely pitted) seeds with free (*vs* fused) caruncle lobes.

Probably not closely related to *C. micrantha s. str.*, which differs in having narrower leaves 0.6–1.6 (*vs* 1.6–2.9) mm wide, shorter racemules 12–40 (*vs* 17–95) mm long with fewer (2–4 *vs* 5–8(–10)) nodes, solitary (*vs* usually paired) flowers, longer pedicels 1.2–2.9 (*vs* 0.3–1.2) mm long, smaller perianths 2.8–4.5 (*vs* 4.5–5.9) mm long, white, erect (*vs* yellow, spreading) staminal filaments and striate seeds (*vs* smooth to finely pitted).

Corynotheca gracilis overlaps in distribution in north-western Australia, but is readily distinguished from *C. divaricata* by the fibrous (*vs* fleshy-fibrous) roots, basal leaves 7–15(–20) (*vs* 14–68) mm long, 0.5–0.8(–1.1) (*vs* 1.6–2.9) mm wide, racemules with 5–8(–10) (*vs* 2–5) nodes, 0.2–0.4 (*vs* 0.4–0.9) mm diam., flowers usually solitary (*vs* usually paired), pedicels 1.0–3.1 (*vs* 0.3–1.2) mm long , seeds 3.4–4.7 (*vs* 2.3–3.7) mm long and striate (*vs* smooth to very finely pitted).

Notes: Previous records for New South Wales were based on misidentifications, including of sterile *Lechenaultia divaricata* F.Muell. Specimens of *C. divaricata* are known from adjacent parts of South Australia, so it may yet be located in far NE New South Wales.

Henderson (1987) noted that *G. Chippendale 4312* might represent a discrete taxon. While the racemules are ±straight in this collection, numerous similar collections are now available and this character is variable, even within individual specimens, so no taxonomic distinction is recognised here, but further field studies may be justified (P. Jobson & D. Albrecht, pers. comm.). Both variants are illustrated in Fig. 2. A variant with striate seeds from central Northern Territory (*D.E. Albrecht 12759 & P.K. Latz*; *D.E. Albrecht 13285 & P.K. Latz*; NT), has not been directly examined (images seen), but may represent a discrete taxon. It is recognised as *Corynotheca micrantha* var. ridged seeds (D.E.Albrecht 12759 & P.K.Latz) by the Northern Territory Herbarium.

Corynotheca elongata (R.J.F.Hend.) R.L.Barrett & T.Macfarlane, *comb. et. stat. nov*.

Basionym: *Corynotheca micrantha* var. *elongata* R.J.F.Hend., *Fl. Austral.* 45: 475, 303, fig. 70h (1987).

Type: St Fergus road, between Toodyay Rd and Avon R., Western Australia, 4 Jan. 1972, *N.T. Burbidge 8012* (holo: PERTH 01115731; iso: CANB 210426, CANB 210427, MEL 222040).

Tufted, tangled, rhizomatous *perennial*, glabrous. *Roots* many, at least 50 mm long, fleshy-fibrous, sand-binding. *Stems* not seen. *Leaves* few, linear-subulate, 5–34 mm long, 0.8–1.7 mm wide, flat, reducing rapidly to bracts upwards, all usually senesced by anthesis. *Inflorescence* perennating, uninterrupted, evenly or somewhat unevenly diffuse, irregularly paniculate, to 60 cm long, dark green; peduncle ascending to decumbent, subterranean at base; major branches outwardly curved to decumbent; lowest branch at least 10 cm from rhizome; panicle branches dichotomously divaricate, each node divaricate at 90–150°; racemules with axis sub-tortuous, 37–78(–200) mm long, with 4–8 nodes, each node diverging at (160–)170–180°, finely ribbed, but otherwise smooth or crenulate; internodes 4–13(–20) mm long, ±straight to curved, 0.2–0.5 mm wide; flowers solitary in branch axils, most developing; lower bracts linear-subulate, 3.5–7 mm long, acuminate; uppermost bracts obovate to ±triangular, 0.5–1.6 mm long; pedicels 0.8–1.9(?–3) mm long. *Perianth* 3.1–4.3 mm long, segments connate for *c*. 0.5 mm, spirally twisting after anthesis, deciduous. *Sepals* ovate, 2.8–4.0 mm long, 1.0–1.3 mm wide, apex apiculate, with a minute appendage *c*. 0.2 mm long, pink to purplish to brown, mostly white adaxially, median band darker abaxially. *Petals* ovate, 2.6–3.5 mm long, 1.0–1.2 mm wide, acute, white to cream, median band greenish. *Filaments* held erect, straight or slightly incurving, 1.8–2.5 mm long, subequal, dilated and minutely papillose, white; anthers 0.5–0.6 mm long. *Style* filiform, to 2.1 mm long, *c*. equalling stamens. *Capsule* erect to pendulous, obpyriform, 3.1–4.2 mm long, 1.8–2.2 mm wide, brown, slightly wrinkled. *Seeds* 1 or 2 per fruit, 1.8–2.7 mm long, *c*. 1.4 mm wide, glossy black to iridescent, longitudinally striate; caruncle conical distally, the lobes fused (Figure 13).

Diagnostic characters: Basal leaves 5–34 mm long; racemules with 4–8 internodes, diverging or straight ((160–)170–180°), internodes 4–13(–20) mm long, 0.2–0.5 mm diam., ±straight; seeds 1.8–2.7 mm long.

Selected specimens examined: WESTERN AUSTRALIA: Ridley Road, 1.2 km SW Mount Billy, 13 Nov. 1996, *M.G. Allen 941* (PERTH); between Perth and York, Nov. 1877, *F. Mueller s.n.* (MEL 107037); Preston and Collie Rivers, 7 Dec. 1877, *F. Mueller s.n.* (MEL 107272); Landsell remnant bushland Popanyinning, 13 Nov. 1996, *A.G. Gunness et al., POPO 15/61* (PERTH); Yanchep National Park: 0.5 mile up track on W side of Loch, 18 Nov. 1963, *A. James 127* (PERTH); Moore River Bridge at junction Lancelin-Gingin road, 30 Nov. 1974, *T.A. Halliday 179* (AK, *n.v.*, CANB, PERTH); Hi Vallee property (D. & J. Williams) Warradarge, close to creekline near E boundary of property, 7 Dec. 2002, *M. Hislop 2904* (PERTH); Greenhills Railway embankment, W of Lott Road, S side Jamieson's land, 16 Jan. 2000, *C. Howell CH 481* (PERTH); 19 km NW Williams to Arthur River, 26 Nov. 1984, *G.J. Keighery 7412* (CANB, PERTH); Wilgie Creek Reserve No. 40339, North Yunderup, 26 Oct. 2000, *P. Payne 11* (PERTH); Reserve A21064 located *c*. 15 km directly NE of Arthur River townsite, 24 Nov. 1998, *L.W. Sage & F. Obbens LWS 1414* (PERTH); Helena Valley, 27 Jan. 2000, *J. Seabrook 517* (CANB); Lake Ronnerup, *c*. 19 km SSW of Lake King townsite, 22 Sept. 2001, *A. Webb & B. Muir 606* (PERTH).

Distribution: From Eneabba south to Dunsborough, inland to near Arthur River and disjunct populations at Lake Coomelberrup 10 km SSE of Dumbleyung, Jilakin Rock, and near Lake King in Western Australia (Fig. 7).

Habitat: Grows on white, grey or yellow sand, often in heath (kwongkan) with *Alexgeorgea nitens*, *Banksia nobilis* subsp. *fragrans*, *B. stenoprion*, *B. tortifolia*, *Calothamnus sanguineus*, *Corymbia calophylla*, *Ecdeiocolea monostachya*, *Eucalyptus accedens*, *E. camaldulensis*, *E. rudis*, *Macrozamia fraseri*, *Melaleuca urceolaris*, *Nuytsia floribunda*, *Schoenus griffinianus*, *Thryptomene hyporhytis*, *Verticordia eriocephala*, *V. grandis* and *V. ovalifolia*.

Phenology: Flowers mostly in November–January.

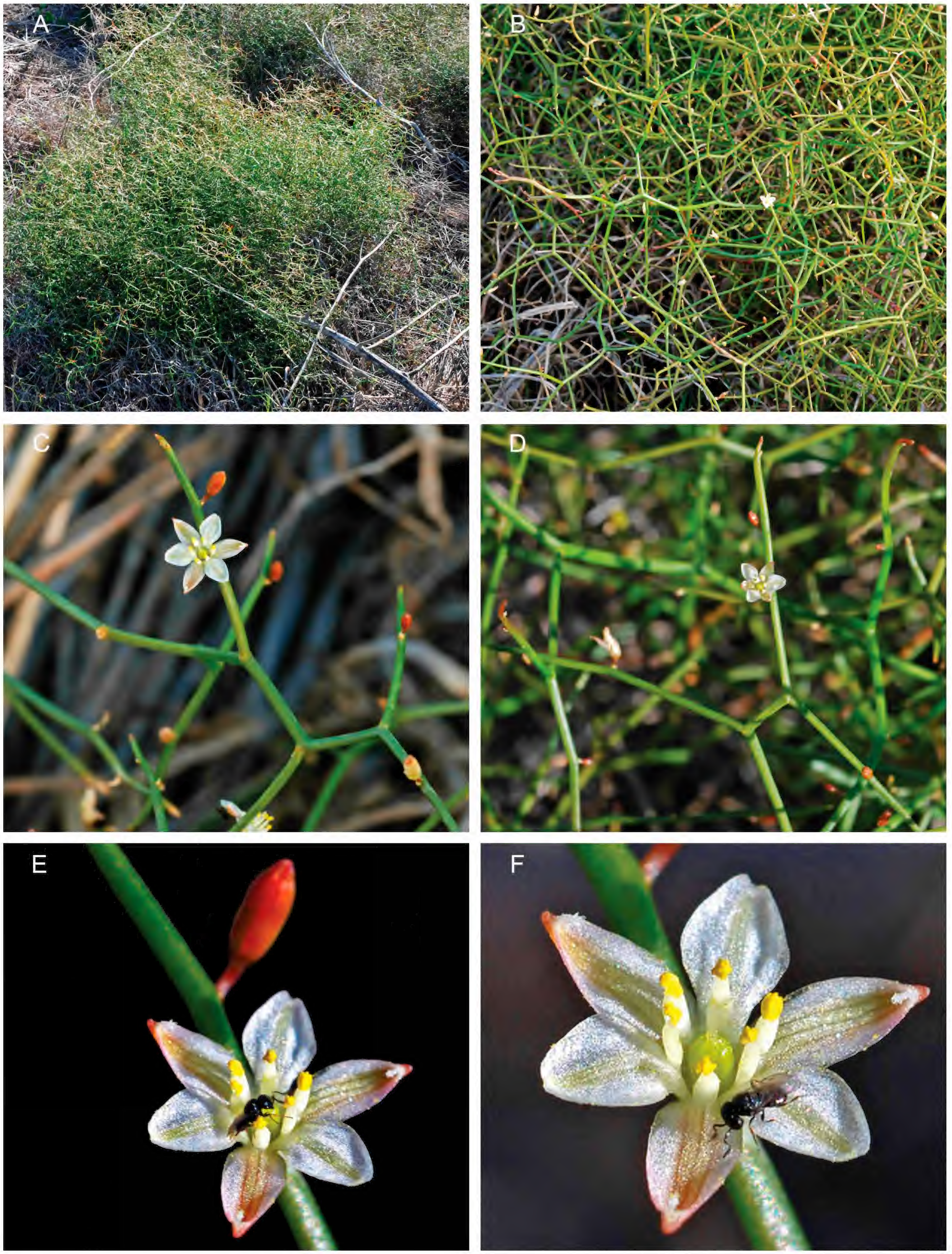

Fig. 13. *Corynotheca elongata*. A. Habit. B. Flowering branches. C, D. Flowering branchlets. E, F. Flowers. Images from Calingiri (not vouchered). Photographs by F.& J. Hort.

Conservation status: *Corynotheca elongata* is widespread and is not currently considered threatened, though numerous roadside populations have been noted to be in decline, especially at the northern end of the species' range (J. Hort, pers. comm.).

Common name: Spreading Sand Lily.

Etymology: The specific epithet is from the Latin *elongatus* (lengthened, elongated), in reference to the elongated ±straight racemules.

Affinities: *Corynotheca elongata* is probably most closely related to *C. panda*, differing in the basal leaves 5–34 (*vs* 45–180) mm long, racemules diverging or straight (160–)170–180° (*vs* diverging at 140–180°), 0.2–0.5 (*vs* 0.3–0.7) mm diam., ±straight (*vs* ±straight to evenly curving) and seeds 1.8–2.7 (*vs* 2.8–3.3) mm long. Possibly also related to *C. pungens,* which has persistent cauline leaves and pungent bracts.

Notes: Henderson (1987) thought that this taxon may merge with *C. panda*, and their geographical ranges do approach each other, but morphological intergradation has not been observed, and their ranges do not actually overlap. The inland populations may warrant further field-based study to assess variation in these isolated populations.

Corynotheca flexuosissima R.J.F.Hend., *Fl. Austral.* 45: 474, 304, figs 70j, 96f, g (1987).

Type: Barrow Is., Western Australia, Oct. 1980, *R. Buckley 7222* (holo: PERTH 115308).

Tufted, tangled, rhizomatous *perennial*, glabrous. *Roots* few, deeply buried, at least 50 mm long, fleshy-fibrous, sand-binding. *Stems* not seen. *Leaves* few, linear-subulate, 12–23 mm long, 0.6–1.1 mm wide, flat, reducing rapidly to bracts upwards, all usually senesced by anthesis. *Inflorescence* perennating, irregularly paniculate, to 60 cm long, light dull green; peduncle ascending to decumbent, long-subterranean at base; major branches decumbent; lowest branch 4–30 cm from rhizome; panicle branches dichotomously divaricate, each node divaricate at 80–150°; racemules with axis tortuous, 4–12(–25) mm long, with (5–)9–20 nodes, each node divaricate at 90–150°, finely ribbed, but otherwise smooth; internodes 0.8–2 mm long, 0.2–0.6 mm wide, straight to gently curving; flowers solitary in branch axils; lower bracts linear-subulate, 5–13 mm long, acuminate; uppermost bracts obovate to ±triangular, 0.3–1.2 mm long; pedicels 0.2–0.9 mm long. *Perianth* 1.4–2.5 mm long, segments connate for *c.* 0.2 mm, spirally twisting after anthesis, deciduous. *Sepals* narrowly ovate to elliptic, 1.3–2.2 mm long, 0.7–0.8 mm wide, apex apiculate, with a minute appendage *c.* 0.1 mm long, margins white, median band greenish to pale brown darker. *Petals* elliptic, 1.2–2.4 mm long, 0.7–0.8 mm wide, acute, white to cream, median band sometimes greenish. *Filaments* held erect, straight or slightly incurving, subequal, 0.6–0.8 mm long, white, minutely papillose; anthers *c.* 0.3 mm long. *Style* filiform, to 0.9 mm long, exceeding stamens. *Capsule* antrorse, ovoid to obovoid, 2.5–3.0 mm long, 1.2–1.7 mm wide, brown, slightly wrinkled. *Seed* 1(2) per fruit, 1.8–2.1 mm long, *c.* 1.3 mm wide, glossy black to iridescent, longitudinally striate; caruncle conical distally, the lobes fused. *2n* = 42 (G.J. Keighery, *Feddes Repert.* 95: 527 (1984); *Wittwer 1783*, as *C. acanthoclada*). (Figures 3a, 14)

Diagnostic characters: Plants with leaves all basal, dry at anthesis, reduced to bracts above, upper bract apices acuminate, but not pungent, inflorescence with a dense, gnarled appearance, racemules 4–12(–25) mm long, 0.2–0.6 mm diam., with (5–)9–20 nodes, internodes 0.8–2 mm long, perianth 1.4–2.1 mm long.

Other specimens examined: WESTERN AUSTRALIA: Barrow Island, Oct. 1980, *R. Buckley 7202* (PERTH); Thevenard Island, N side 1 km from W end, 30 June 1988, *H. Butler & V. Long VL 275* (PERTH); Thevenard Island, 15 May 1954, *W.H. Butler 10899/63* (PERTH); NW Cape, near Lighthouse, 1 Jan. 1961, *A.S. George 2302* (PERTH); Vlaming Head, E of lighthouse, 24 May 1965, *A.S. George 6587* (PERTH); 4–5 miles N of Yardie Creek, 27 May 1965, *A.S. George 6657* (PERTH); *c.* 6 miles N of Yardie Creek, W of Cape Range, 6 Sept. 1970, *A.S. George 10309* (CANB, MEL, PERTH); Long Island [Serrurier Island], Onslow, 31 July 1963, *D.W. Goodall 584* (PERTH); Cape Range Peninsula, W coastal area, 1 Oct. 1995, *S. Hunger & N. Kilian 4175* (PERTH); Cape Range Peninsula, North West Cape, coastal area, 2 Oct. 1995, *S. Hunger & N. Kilian 4181* (PERTH); Boodie Island, off southern tip of Barrow Island, Pilbara Coast, 26 Oct. 2000, *K.F. Kenneally 11628* (CANB, PERTH); Long Island, NW of Onslow [Serrurier Island], 23 May 1960, *R.D. Royce 6337* (PERTH); Thevenard Island, NW of Onslow, 24 May 1960, *R.D. Royce 6357* (PERTH); 60 m S of navigation tower at W end of [Thevenard] Island, 23 May 1990, *M. White MRW 037* (PERTH); Vlaming Head, 9 Aug. 1976, *E. Wittwer W 1783* (PERTH).

Distribution: Restricted to a small area from Cape Range to Onslow on the mainland, and a few offshore islands north to Boodie and Barrow Islands in Western Australia (Figure 8A).

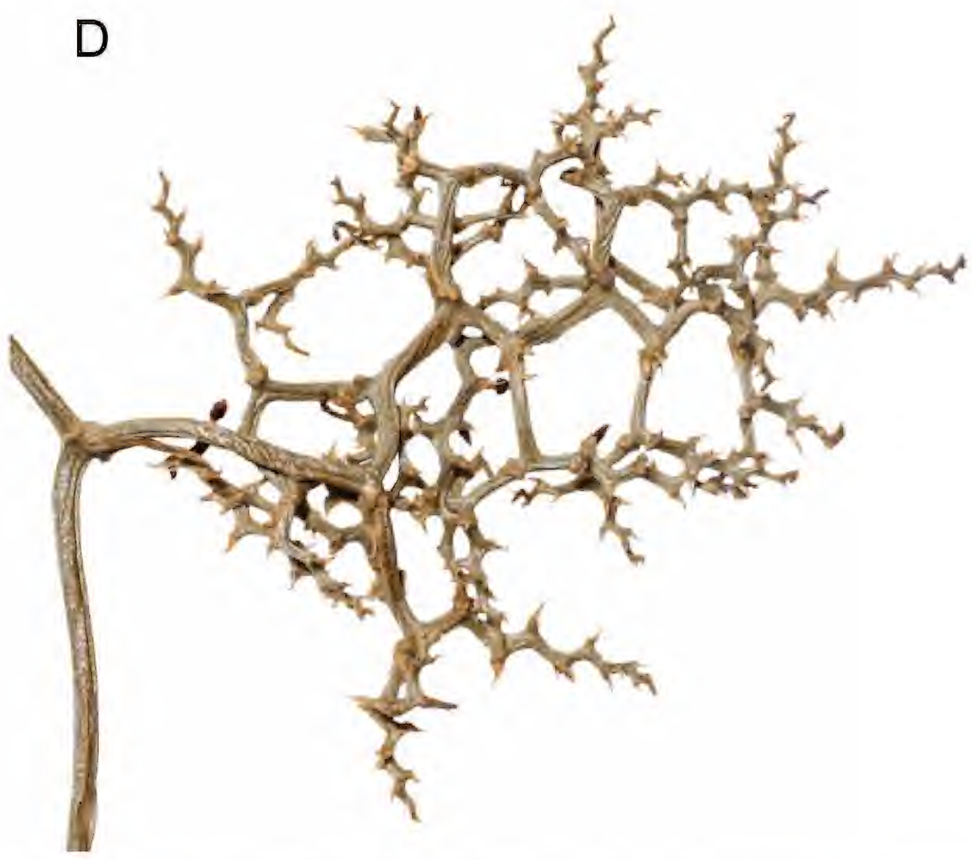

Fig. 14. *Corynotheca flexuosissima*. A. Habitat on Serrurier Island. B. Flowering branches. C–E. Racemules. F. Flower. Images from Serrurier Island (not vouchered) (A, E, F); Voucher: Boodie Island, *K.F. Kenneally 11628* (CANB) (B–D). Photographs by V. Long (A, E, F); R.L. Barrett (B–D).

Habitat: Grows on beach sand and coastal limestone in stunted grassland and open low shrubland with *Acacia ampliceps*, *A. bivenosa*, *A. sclerosperma*, *Amaranthus undulatus*, *Arivela viscosa*, *Boerhavia coccinea*, *Commicarpus australis*, *Cynanchum viminale* subsp. *australe*, *Enneapogon caerulescens*, *Eragrostis falcata*, *Eulalia aurea*, *Euphorbia trigonosperma*, *Salsola australis*, *Scaevola cunninghamii*, *S. spinescens*, *Spinifex longifolius* and *Triodia* spp.

Phenology: Flowers mostly May–July(–October).

Conservation status: Restricted in distribution in a region with several active developments, *Corynotheca flexuosissima* is recommended for listing as a Priority 4 taxon in Western Australia and assessment of population sizes should be undertaken to determine long-term risks to this species.

Common name: Compact Zigzag Lily.

Etymology: The specific epithet is from the Latin *flexuosus* (flexuose, zigzag) and the termination *-issimus* (extremely, remarkably), in reference to the compact, zigzag racemule axes.

Affinities: *Corynotheca flexuosissima* is most likely to be confused with *C. asperata* and *C. dichotoma* based on the compact inflorescence of each species. *Corynotheca asperata* is very distinctive in having finely scabrid (*vs* glabrous) stems, fibrous (*vs* fleshy-fibrous) roots and racemules with (0)1–6 (*vs* (5–)9–20) nodes. *Corynotheca dichotoma* can be readily distinguished from *C. flexuosissima* by the more openly branching racemules 15–60 (*vs* 4–12(–25)) mm long, with (1–)5–13 (*vs* (5–)9–20) nodes, internodes 1–7 (*vs* 0.8–2) mm long, longer peduncles 0.8–2.3 (*vs* 0.2–0.9) mm long and larger perianth 4.1–5.0 (*vs* 1.4–2.5) mm long.

Notes: It is interesting to note that most known populations are on islands, or in rocky environments on the Cape Range, and it may be fire sensitive, or very specific to coastal limestone soils.

Corynotheca gracilis (R.J.F.Hend.) R.L.Barrett & T.Macfarlane, *comb. et stat. nov.*

Basionym: *Corynotheca micrantha* var. *gracilis* R.J.F.Hend., *Fl. Austral.* 45: 475, 302–303, fig. 96c–e (1987).

Type: behind Riddle Beach, 5 km SW of Broome townsite, S Kimberley, Western Australia, 17 June 1984, *K.F. Kenneally 9025* (holo: PERTH 1115715; iso: BRI AQ0433514, CANB 379419).

Illustrations: Rye (1992; fig. 299f); Kenneally *et al.* (1996; pl. p. 200).

Tufted, tangled, rhizomatous *perennial*, glabrous. *Roots* many, 50–150 mm long, to 2.0 mm thick, fibrous, sand-binding. *Stems* short, to 10 mm long and 6 mm wide. *Leaves* few, linear-subulate, 7–15(–20) mm long, to 0.8(–1.1) mm wide, flat, reducing rapidly to bracts upwards, all usually senesced by anthesis. *Inflorescence* perennating, irregularly paniculate, 30–150 cm long, dark green; peduncle ascending (sometimes decumbent at length), subterranean at base; major branches erect to ascending; lowest branch 1.5–8 cm from rhizome; panicle branches dichotomously divaricate, each node divaricate at 90–150°; racemules with axis not or slightly tortuous, 20–60 mm long, with 2–5 nodes, each node divaricate at 110–140°; finely ribbed, but otherwise smooth; internodes 5–23 mm long, 0.2–0.4 mm wide, ±straight; flowers solitary in branch axils, few–most developing; lower bracts ±triangular, 5–12 mm long; uppermost bracts ±triangular, 0.9–1.3 mm long, acuminate; pedicels 1.0–3.1 mm long. *Perianth* 4.0–6.5 mm long, segments connate for *c.* 0.5 mm, spirally twisting after anthesis, deciduous. *Sepals* narrowly elliptic to narrowly oblong-elliptic, 2.7–6.1 mm long, 1.1–1.4 mm wide, apex apiculate, with a minute appendage *c.* 0.15 mm long, margins white, median band brown. *Petals* narrowly oblong to narrowly elliptic, 4.0–5.8 mm long, 1.4–1.5 mm wide, obtuse, white to cream, median band cream to brown, slender. *Filaments* slightly spreading, straight or slightly incurving, 1.9–4.0 mm long, unequal, dilated and minutely papillose in lower 1/2 to 3/4, yellow; anthers 0.6–0.7 mm long. *Style* filiform, to 4.4 mm long, subequal to or exceeding stamens. *Capsule* antrorse, fusiform to obpyriform to obovate, 5.5–9.5 mm long, 2.5–3 mm wide, brown, slightly wrinkled. *Seed* 1(2) per fruit, 3.4–4.7 mm long, *c.* 1.8 mm wide, glossy black to brown, longitudinally striate; caruncle conical distally, blackish, the lobes fused (Figures 4c, 15).

Diagnostic characters: Basal leaves 7–15(–20) mm long, racemule internodes diverging at 80–100°, 0.2–0.4 mm wide, pedicels 0.9–1.3 mm long, perianth 4.0–6.5 mm long, staminal filaments 1.4–2.1 mm long, seeds 3.4–4.7 mm long.

Fig. 15. *Corynotheca gracilis*. A. Habit. B, C. Flowering branchlet. D–G. Flowers. H. Fruit; I. Seed. Vouchers: A–C, E: Roebuck Bay, Broome (not vouchered); D, F–H: north of Ngumban Cliffs, *M.D. Barrett, R.L. Barrett & B. Anderson MDB 4193* (PERTH); and I: Broome, *P.R. Foulkes* 46 (PERTH). Scale = 1 mm. Photographs by R.L. Barrett.

Selected specimens examined: WESTERN AUSTRALIA: 45 km W of Sandfire Roadhouse on [Great Northern] Highway, 3 Sept. 1993, *C.R. Alcock 11392* (AD, PERTH); *c.* 3 km SE of Ngumban Cliffs, 5 Apr. 2013, *M.D. Barrett*, *R.L. Barrett* & *B. Anderson MDB 4193* (PERTH); Gary Junction Road, 77.7 km W of Kiwirrkura, 15 Sept. 2015, *R. Butcher et al. RB 2081* (CANB, DNA, PERTH); Beagle Bay [Cape Leveque] Road, 10.5 km N of Great Northern Highway, 31 July 1974, *G.W. Carr 4399 & A.C. Beauglehole 48177* (CANB, PERTH); 'Robert', northern Great Sandy Desert, 31 Aug. 2001, *C.P. Campbell 3721* (PERTH); 25 km N of Broome, Dampier Peninsula, 4 June 1989, *B.J. Carter 400* (DNA, PERTH); Canning Stock Route, near Durba Spring, 26 Aug. 1995, *M.G. Corrick 11136* (CANB, MEL, PERTH); Rudall River National Park, towards E boundary and S of main track, 22 July 2003, *D.J. Edinger & G. Marsh DJE 3660* (PERTH); Broome area, 13 Oct. 1984, *P.R. Foulkes 46* (PERTH); Near Sally May well site, Great Sandy Desert, 28 June 2009, *G.F. Griffin & S.R. Dunlop GSD 09-117* (PERTH); Gogo Station, 8 Oct. 1952, *K. Fitzgerald 1* (PERTH); Site D1, near Edgar Range, SE of Broome, 13 Aug. 1976, *K.F. Kenneally 5655* (CANB, PERTH); 4 km S of Cape Bertholet, Dampierland, N of Broome, 20 Apr. 1977, *K.F. Kenneally 6075* (CANB, PERTH); 156 km SW of Halls Creek, 5 July 1989, *K.F. Kenneally s.n.* (BRI, PERTH); Myroodah Station, Oct. 2011, *P. Knapton 23* (PERTH); 99 km E of Fitzroy Crossing, 1 July 1983, *C. MacDonald 420* (BRI); Dampier's Land near Broome, July 1911, *E. Mjöberg s.n.* (NSW); 100 km E of Fitzroy Crossing along the Great Northern Highway, 12 Sept. 1982, *N.F. Norris* 872 (CBG, MEL, NSW, PERTH); *c.* 10 km SW of Mandora Homestead near the top of a pindan rise, 5 Apr. 1995, *H. Pringle PRP326* (PERTH); Roebuck Bay, May 1890, *J.G.O. Tepper 125* (AD, *n.v.*, MEL); 1 km S of Broome Bird Observatory, *c.* 25 km from Broome, 25 June 1997, *T.L. Woodburn s.n.* (CANB).

Distribution: Scattered but relatively common from Broome and Mandora in the west, north to Ngumban Cliffs, ENE of Fitzroy Crossing and south east to Kiwirrkura in Western Australia (Figure 8A).

Habitat: Grows on red sand flats and commonly on sand dunes, usually on deep sands. Associated species include *Acacia eriopoda*, *A. hippuroides*, *A. monticola*, *A. tumida* var. *kulparn*, *Chamaecrista symonii*, *Corymbia chippendalei*, *C. polycarpa*, *C. zygophylla*, *Dicrastylis doranii*, *Eragrostis falcata*, *Gyrostemon tepperi*, *Jacksonia aculeata*, *Melaleuca lasiandra*, *Newcastelia cladotricha*, *Scaevola parvifolia*, *Solanum cunninghamii*, *Triodia basedowii*, *T. bitextura*, *T. pungens* and *Ventilago viminalis*.

Phenology: Flowers mostly between June and October, but also as early as March.

Conservation status: *Corynotheca gracilis* is widespread and is not currently considered threatened.

Common name: Slender Zigzag Lily.

Etymology: The specific epithet is from the Latin *gracilis* (slender, fine), in reference to the slender inflorescence branches.

Affinities: *Corynotheca gracilis* is closely related to *C. borealis*, differing in the racemule internodes diverging at 110–140° (*vs* 80–100°); pedicels 1.0–3.1 (*vs* 0.9–1.3) mm long; sepals 1.1–1.4 (*vs* 0.8–0.9) mm wide, petals 1.4–1.5 (*vs* 0.7–0.8) mm wide and staminal filaments 1.9–4.0 (*vs* 1.4–2.1) mm long.

This pair may have affinity to the only other tropical species, *C. lateriflora* (R.Br.) F.Muell. ex Benth. rather than *C. micrantha* (Lindl.) Druce based on the larger perianth, seeds and tropical distribution. *Corynotheca gracilis* can be readily distinguished from *C. lateriflora* by the racemules with axis not or slightly tortuous (*vs* tortuous), 20–60 (*vs* 65–175(–250)) mm long, with 2–5 (*vs* 4–7) nodes, each node divaricate at 110–140° (*vs* diverging at 170–180°) and internodes 5–23 (*vs* 7–31(–40)) mm long.

Corynotheca gracilis differs from *C. micrantha* by the fleshy-fibrous roots (*vs* fibrous), basal leaves 7–15(–20) (*vs* 28–105) mm long, racemule internodes diverging at 110–140° (*vs* 130–180°), 0.2–0.4 (*vs* 0.3–0.6) mm wide, perianth 4.0–6.5 (*vs* 2.8–4.5) mm long, staminal filaments 1.9–4.0 (*vs* 1.7–2.1) mm long and seeds 3.4–4.7 (*vs* 2.3–3.4) mm long.

Notes: Henderson (1987) commented that "this taxon may prove to be specifically distinct from *C. micrantha*." A larger range of available specimens has enabled both taxa to be refined in circumscription and distribution, and species rank is considered appropriate for Henderson's variety.

Corynotheca lateriflora (R.Br.) F.Muell. ex Benth., *Fl. Austral.* 7: 49–50 (1878); *Caesia lateriflora* R.Br., *Prodr.* 277 (1810).

Type: Carpentaria Is. h & g [North Is. and Vanderlin Is., Sir Edward Pellew Group, Northern Territory], 16–26 December 1802, *R. Brown* [*Bennett no. 5691*] (lectotype designated by R.J.F.Henderson, *Fl. Austral.* 45: 474 (1987): BM 000990667 (right hand piece)*; presumed isolecto: BM 000990664*, BM 000990665*, BM 000990666*, BRI AQ0022990, CANB 279207, G 00165666*, K 000794734*, MEL 107057, MEL 107058, P 00852453*, P 00852454*, P 00852455*).

Illustrations: Henderson (1987; figs 70d, 96a).

Tufted, tangled, rhizomatous *perennial*, glabrous. *Roots* many, 50–120 mm long, thin fleshy-fibrous, not sand-binding. *Stems* to 30 mm long and 7 mm diam. *Leaves* several, linear-subulate, (40–)120–220 mm long, 0.6–2.2 mm wide, flat to convolute, reducing rapidly to bracts upwards, all usually senesced by anthesis. *Inflorescence* perennating, irregularly paniculate, to 75(–100) cm long, grey-green to dark green; peduncle erect to ascending, subterranean at base; major branches spreading to decumbent; lowest branch 2–5(–11) cm from rhizome; panicle branches divergent, each node divergent at 90–150°; racemules with axis tortuous, 65–175(–250) mm long, with 4–7 nodes, each node diverging at 170–180°, finely ribbed, but otherwise smooth; internodes 7–31(–40) mm long, 0.1–0.6 mm wide, ±straight; flowers solitary in branch axils; lower bracts linear-subulate, 16–50 mm long, acuminate, sometimes stiff; uppermost bracts ovate-attenuate, 1.2–5.1 mm long; pedicels 1.4–2.0(–3.0) mm long. *Perianth* 6.5–8.0 mm long, segments connate for *c*. 0.6 mm, spirally twisting after anthesis, deciduous. *Sepals* linear to narrowly oblong, 6.4–7.9 mm long, 1.1–1.6 mm wide, apex apiculate, with a minute appendage *c*. 0.6 mm long, margins white, median band darker, pink to purplish to brown. *Petals* narrowly elliptic, 6.2–7.8 mm long, 1.6–2.0 mm wide, emarginate, margins white to cream, median band darker, pale mauve or pink. *Filaments* slightly spreading, kinked to almost straight, unequal, 3.2–4.1 mm long, dilated and minutely papillose, yellow; anthers 0.7–1.0 mm long. *Style* filiform, to 4.2 mm long, subequal to exceeding stamens. *Capsule* erect to pendulous, clavate-attenuate, 7–15 mm long, 2.0–4.1 mm wide, brown, slightly wrinkled. *Seed* 1(2) per fruit, 5.0–6.8 mm long, 1.8–2.0 mm wide, glossy black to iridescent, longitudinally striate; caruncle conical distally, the lobes free (Figures 4a, 16).

Diagnostic characters: Leaves (40–)120–220 mm long, perianth 6.5–8.0 mm long, seeds 5.0–6.8 mm long.

Selected specimens examined: NORTHERN TERRITORY: 10 July 1972, 37 miles S of Oenpelli, 10 July 1972, *L.G. Adams 2794* (CANB, DNA, *n.v.*); Boggy Plain Creek near Jabiru, 21 Feb. 1973, *L.G. Adams 3051* (BRI, CANB, DNA, *n.v.*, NSW); near Finnis River, 9 Sept. 1946, *S.T. Blake 16748* (CANB, DNA, *n.v.*); 8 miles NE of Wangi Homestead, 26 Aug. 1969, *N. Byrnes 1673* (BRI, CANB, CBG, DNA, *n.v.*, MEL, NSW); *c*. 22.4 mi. SE of Darwin, 27 May 1958, *G. Chippendale 4480* (DNA, *n.v.*, NSW); Arnhem Land. *c*. 18 km ESE of Ramingining, 21 June 2001, *I.D. Cowie 9408* (BRI, CANB, DNA, *n.v.*, MEL); west side of South West Island, Sir Edward Pellew Group, 9 Feb. 1976, *L.A. Craven 3734* (CANB, DNA, *n.v.*); 10 km south-east of Nourlangie Ranger Station on Pine Creek road, 21 May 1980, *L.A. Craven 5702* (BRI, CANB, DNA, *n.v.*, MEL); Tabletop Range, 19 May 1985, *C.R. Dunlop 6792* (DNA, *n.v.*, MEL, RSA, *n.v.*); *c*. 43.9 km NNE of Pungalina Homestead on Skeleton Creek Road from Calvert River mouth to Robson River mouth on Pungalina/Seven Emu Wildlife Sanctuary, 25 July 2012, *R. Jensen 2707 & J. Kemp* (BRI); Mount Brockman Outlier 15 km SE of Jabiru along Baroalba Creek, 20 Apr. 1989, *R.W. Johnson 4719* (AD, *n.v.*, BRI, CANB, DNA, *n.v.*, NSW); 44 km SE Oenpelli, 15 June 1978, *P.K. Latz 7803* (AD, *n.v.*, CANB, DNA, *n.v.*); Goyder River Crossing, 16 June 1972, *J.R. Maconochie 1476* (AD, *n.v.*, CANB, DNA, *n.v.*, MEL, PERTH); Gulf of Carpentaria, 1856, *F.Mueller s.n.* (MEL 0107071); Koongara, 16 Apr. 1979, *B.L. Rice 3132* (BRI, DNA, *n.v.*); Kakadu National Park, Upper Koolpin Creek, 9 June 1988, *J. Russell-Smith & D. Lucas 5537* (BRI, CANB, DNA, *n.v.*); Oenpelli Reserve, 26 Apr. 1980, *D. Smyth OP 10.7* (BRI); Oenpelli, 24 Sept. 1948, *R.L. Specht 1057* (AD, *n.v.*, BRI, CANB, MEL, NSW, PERTH); Vanderlin Island, 2 km E of Lake Eams, Sir Edward Pellew Group, 23 July 1988, *B.G. Thomson 2490* (BRI, DNA, *n.v.*, NT, *n.v.*); Little Nourlangie Rock, 7 May 1983, *K.L. Wilson 5195 & C. Dunlop* (DNA, *n.v.*, MEL, NSW).

Distribution: Endemic to the Northern Territory with two disjunct regions of distribution in the 'Top End' and near the Queensland border in the Gulf of Carpentaria (Figure 8A).

Habitat: Grows on damp white, grey or yellow sands along creek margins, on flats and around sandstone outcrops in woodland with *Acacia* sp., *Alphitonia* sp., *Aphyllodium biarticulatum*, *Aristida holathera*, *Banksia dentata*, *Centrolepis exserta*, *Corymbia ferruginea*, *Drosera* sp., *Eragrostis* sp., *Eriachne burkittii*, *E. triseta*, *Eucalyptus miniata*, *E. tetrodonta*, *Eulalia* sp., *Grevillea pteridifolia*, *Hibbertia complanata*, *Leschenaultia* sp., *Melaleuca nervosa*, *Mitrasacme* sp., *Pandanus spiralis*, *Phyllanthus* sp., *Pteris platyzomopsis*, *Sacciolepis myosuroides*, *Schizachyrium* sp., *Spermacoce* sp., *Triodia lanosa*, *Utricularia* sp. and *Uvedalia linearis* var. *lutea*.

Phenology: Flowers mostly February–July, but recorded all year round.

Conservation status: *Corynotheca lateriflora* is widespread and is not currently considered threatened.

Common name: Club-fruit Lily, Sand Lily.

Etymology: The specific epithet is from the Latin *lateri-* (at the side) and *flora* (flower), in reference to the subsessile flowers that appear lateral to the racemules.

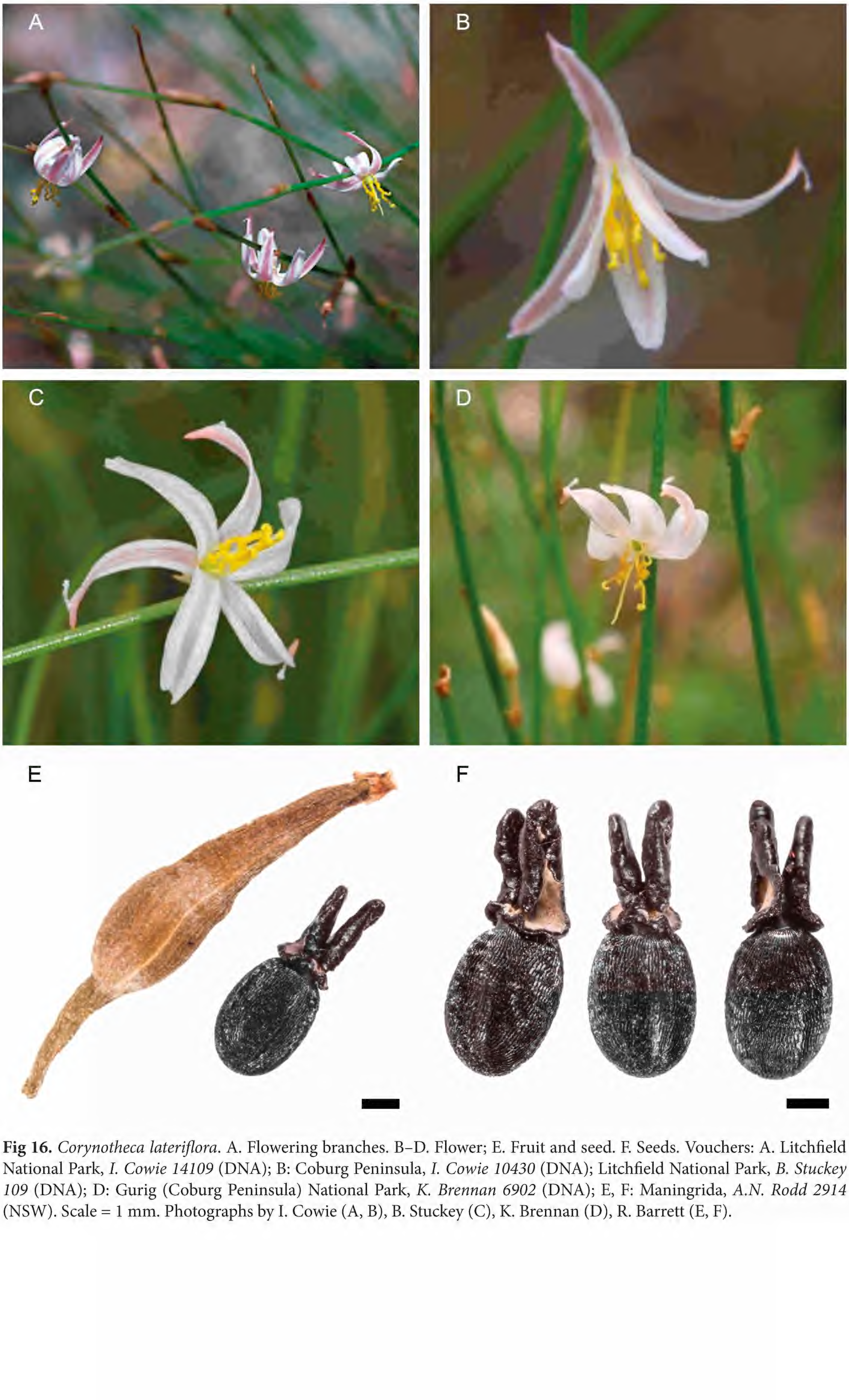

Fig 16. *Corynotheca lateriflora*. A. Flowering branches. B–D. Flower; E. Fruit and seed. F. Seeds. Vouchers: A. Litchfield National Park, *I. Cowie 14109* (DNA); B: Coburg Peninsula, *I. Cowie 10430* (DNA); Litchfield National Park, *B. Stuckey 109* (DNA); D: Gurig (Coburg Peninsula) National Park, *K. Brennan 6902* (DNA); E, F: Maningrida, *A.N. Rodd 2914* (NSW). Scale = 1 mm. Photographs by I. Cowie (A, B), B. Stuckey (C), K. Brennan (D), R. Barrett (E, F).

Affinities: *Corynotheca lateriflora* is readily distinguished from all other species in the genus by the large perianth 6.5–8.0 (*vs* 1.4–6.5) mm long and seeds 5.0–6.8 (*vs* 1.8–4.7) mm long.

Possibly most closely related to *C. licrota* which differs in having fibrous (*vs* fleshy-fibrous) roots, persistent (*vs* dry at anthesis) basal leaves 2.5–4.1(–9) (*vs* 0.6–2.2) mm wide, 5–17 (*vs* 4–7) nodes per racemule, racemules 0.4–1.3 (*vs* 0.1–0.6) mm diam., perianths 4.3–6.0 (*vs* 6.5–8.0) mm long, and seeds 3.0–4.3 (*vs* 5.0–6.8) mm long with colliculate (*vs* folded) caruncle lobes .

Notes: While Mueller (1870: 68) suggested this species might be best placed in *Corynotheca*, the combination was only validated by Bentham (1878: 49).

Robert Brown's unpublished collection notes indicate that he observed this species on both Carpentaria Islands 'h' and 'g' [North Is. and Vanderlin Is. in the Sir Edward Pellew Group], but the available specimens do not indicate whether collections were made on both islands, or only one. For this reason, Henderson (1987: 474) selected a single piece on a single sheet at BM as the lectotype. It is presumed that some, or possibly all, of the additional sheets are therefore isolectotypes, but we cannot be certain given this history.

Many early treatments included *Corynotheca licrota* under *C. lateriflora*, the two first being separated at varietal rank by Gauba (1948) and subsequently separated at species rank by Henderson (1987).

The stems and leaves are recorded as being used to flavour meat during cooking in the Northern Territory (Smith 1991). The collection *D. Smyth OP 10.7* is recorded as being utilised as a seasoning called *Manbunbarra* near Oenpelli. Similarly, oral history records that *Corynotheca licrota* was called *Bunbarr* by the Bininj Kunwok people of West Arnhem Land, and used as a herb to cook emu in ground ovens (Nakardbam 2013).

Previous records from Western Australia are referable to either *C. borealis* or *Tricoryne* sp. Kimberley (K.F. Kenneally 4857).

Corynotheca licrota R.J.F.Hend., *Fl. Austral.* 45: 474, 300–301, figs 70e, 96b (1987); *Corynotheca lateriflora* var. *laevisperma* Gauba, *Vict. Nat.* 65: 111, 113 (1948).

Type: Mount Dispersion, Murray River, New South Wales, December 1853, *F. Mueller s.n.* (holo: MEL 107234).

Possible isotypes: 'Murray', *F.Mueller* (?iso: MEL 106891); 'Sandridges on the River Murray', *F.Mueller* (?iso: MEL 107232).

Corynotheca lateriflora auct. non (R.Br.) F.Muell. ex Benth.; E.Gauba, *Vict. Nat.* 65: 111 (1948), *p.p.*; J.P.Jessop in J.P.Jessop & H.R.Toelken (eds), *Fl. S. Austral.* Edn. 4, 4: 1752 (1986), *p.p.*

Illustrations: Gauba (1948; fig. p. 112), as *C. lateriflora*; Cunningham *et al.* (1981; pl. p. 183), as *C. lateriflora*; Henderson (1987; figs 70e, 96b).

Tufted, erect, rhizomatous *perennial*, glabrous. *Roots* many, 40–80 mm long, fibrous, not sand-binding. *Stems* short, to 5 mm long and 2.5 mm diam. *Leaves* several, linear-subulate, 50–300(–600) mm long, 2.5–4.1(–9) mm wide, flat or complicate, reducing rapidly to bracts upwards, persistent, basal, erect. *Inflorescence* perennating, irregularly paniculate, to 70 cm long, bright green; peduncle erect to ascending, subterranean at base; major branches divergent; lowest branch 10–25 cm from rhizome; panicle branches diverging, each node diverging at 130–160°; erect to ascending; racemules with axis tortuous, 75–300 mm long, with 5–17 nodes, each node continuous (at ±180°), finely ribbed, but otherwise smooth; internodes 4–25 mm long, 0.4–1.3 mm wide, ±straight; flowers solitary (rarely 2) in branch axils; lower bracts linear-subulate, 40–200 mm long, acuminate; uppermost bracts ovate-attenuate, 1.5–7 mm long; pedicels 1.2–2.6 mm long. *Perianth* 4.3–6.0 mm long, segments connate for *c.* 0.4 mm, spirally twisting after anthesis, deciduous. *Sepals* narrowly oblong, 4.0–5.9 mm long, 0.9–1.1 mm wide, apex apiculate, with a minute appendage *c.* 0.8 mm long, white to pink to purplish to brown, median band darker. *Petals* narrowly elliptic, 3.9–5.5 mm long, 0.7–0.9 mm wide, emarginate, white to cream, median band darker. *Filaments* slightly spreading, straight, subequal, 1.7–2.2 mm long, dilated and minutely papillose, yellow; anthers 0.5–0.8 mm long. *Style* filiform, to 3.8 mm long, exceeding stamens. *Capsule* pendulous, ovoid to obovoid, 2.8–7.5 mm long, 2.1–2.8 mm wide, brown, slightly wrinkled. *Seeds* 1–5 per fruit, 2.7–4.3 mm long, 1.3–1.5 mm wide, glossy black to iridescent, smooth to finely longitudinally striate; caruncle spreading distally, the lobes free, folded, antler-like (Figure 17).

Diagnostic characters: Mature basal leaves persistent at anthesis, 2.5–4.1(–9) mm wide, inflorescence axes and racemules smooth, finely ribbed, racemules consistently continuous at ±180, pedicels 1.2–2.6 mm long, caruncle lobes on seeds free.

Fig. 17. *Corynotheca licrota*. A–C. Habit. D. Flowering racemule. E. Fruit. F. Seed with antler-like caruncle. Vouchers: A, E: Berri, *M.J. Thorpe 368* (AD); B, D: Mamungari, *D.E. Murfet 7736* (AD); C: Mt Finke, *D.J. Duval 1672* (AD); F: *D.J. Duval 877* (AD). Scale = 1 mm. Photographs by the South Australian Seeds Conservation Centre (D. Duval).

Selected specimens examined: WESTERN AUSTRALIA: West end of Rawlinson Ranges, 72 km WNW of Warrakuma settlement, 17 Aug. 2016, *P.K. Latz 30876* (NT); NORTHERN TERRITORY: Finke River, 1880, *F.A.H. Kempe 371 E* (MEL 107275, MEL 107059); Erldunda Station, 26 Apr. 1974, *P.K. Latz 4970* (AD, *n.v.*, BRI, NT, *n.v.*, PERTH); Hermannsburg Mission, Finke Gorge, 1 Oct. 1977, *P.K. Latz 7506* (AD, *n.v.*, NT, *n.v.*, PERTH); 7 km NW Rainbow Valley visitors centre, 11 Nov. 2012, *P.K. Latz & S.M. Pullyblank 27529* (BRI, *n.v.*, NSW, NT, *n.v.*); 42 km E of Henbury Homestead, Northern boundary, 19 Feb. 2013, *P.K. Latz & A. Schubert 27692* (NSW, NT, *n.v.*); QUEENSLAND: 'Gilruth Plains', Cunumulla, 29 Sept. 1941, *G.H. Allen 191* (CANB); 'Gilruth Plains', Cunumulla, 8 Sept. 1942, *G.H. Allen 425* (CANB); SW of Charleville, 1 Dec. 1935, *S.L. Everist 1417* (BRI); Thylungra, *c.* 75 mi. NW of Quilpie, 11 Oct. 1955, *S.L. Everist 5706* (BRI, CANB); 7 km E of Gilruth Plains, 6 Oct. 1984, *R.W. Purdie 2166* (BRI); SOUTH AUSTRALIA: 2 miles N of Ooldea, 13 Oct. 1956, *N. Forde 675* (CANB); Loveday, 20 Dec. 1944, *E. Gauba s.n.* (MEL); *c.* 5 km NE of Overland Corner, 15 Nov. 2005, *D.E. Symon 17235* (AD, *n.v.*, MEL); NEW SOUTH WALES: 6.9 km E of Nulty Springs junction, ESE of Enngonia, 18 Sept. 2004, *A.R. Bean 23109* (BRI); Nulty Springs, 20 Nov. 1975, *G.M. Cunningham 4175* (CANB, NSW); E of Narran Lake, near Brewarrina, 22 Nov. 1967, *D.J. McGillivray 2924* (NSW); *c.* 40 km SE of Louth, 19 Nov. 1975, *C.W.E. Moore 7192* (CANB); 'Tuudulya', *c.* 40 km SE of Louth, 9 Oct. 1981, *C.W.E. Moore 8289* (CANB); 70 km NW of Balranald, Nov. 1974, *W.E. Mulham W 830, 835* (CANB, NSW); Pan Ban Station, 22 Oct. 1985, *B.L. Rice 4215* (NSW); Pan Ban Station, 17 Nov. 1985, *B.L. Rice 4298* (BRI); Cobb Highway, 24 km SSE of Barrier Highway, 2 Nov. 1986, *A.N. Rodd, J. Gentle & P.G. Wilson 5821* (AD, NSW); 'Petro', 40 miles NE of Mildura, Site 1, 6 Dec. 1978, *W.S. Semple 832* (NSW); VICTORIA: Hattah Lakes National Park, near old highway and NW of Lake Hattah, 16 Oct. 1960, *A.C. Beauglehole 39276 & J.H. Willis* (MEL); Between Sunset Tank and Monkeytrail Tank, 15 Nov. 1986, *D.C. Cheal s.n.* (MEL 687803); Murray Sunset National Park, beside Rocket Lake, about midway along and *c.* 60 m E from the eastern 'shore', 24 Nov. 2011, *N.G. Walsh 7479, J.L. Birch, C.L. Gallagher & S. Stewart* (CANB, MEL, PAL, *n.v.*, S, *n.v.*).

Distribution: Relatively widespread in the arid zone of southern Australia, in all mainland states, with three somewhat disjunct population areas in the central ranges, Murray-Darling Basin and in southern South Australia. This species has a somewhat remarkable distribution in eastern Australia that clearly tracks the drainage of the Darling and lower Murray Rivers, suggesting possible hydrochory (distribution of seed by water) from inland Australia (Figure 8B).

Habitat: Grows on sand dunes, sandy plains or occasionally on shallow sand over quartzite with *Acacia ligulata*, *A. melleodora*, *A. spondylophylla*, *Actinotus paddisonii*, *Allocasuarina decaisneana*, *Angophora melanoxylon*, *Aristida holathera*, *Austrostipa* sp., *Babingtonia behrii*, *Calandrinia balonensis*, *Calotis erinacea*, *Chrysocephalum apiculatum*, *Codonocarpus cotinifolius*, *Crinum flaccidum*, *Dicrastylis costelloi*, *Dodonaea viscosa*, *Enchylaena tomentosa*, *Eragrostis eriopoda*, *Eremophila willsii*, *Eucalyptus dumosa*, *E. gamophylla*, *E. incrassata*, *E. melanophloia*, *E. socialis*, *Gnephosis tenuissima*, *Grevillea juncifolia*, *Leptospermum coriaceum*, *Phyllota pleurandroides*, *Ptychosema stipulatum*, *Sclerolaena diacantha*, *S. obliquicuspis*, *Swainsona microphylla*, *Triodia basedowii*, *T. irritans*, *T. marginata*, *T. mitchellii*, *T. pungens* and *T. scariosa*.

Phenology: Flowers mostly September–February, but also recorded in April and August following rainfall.

Conservation status: While *Corynotheca licrota* is widespread as a species, it is only known from a single collection in Western Australia where it is recommended for listing as a Priority 1 taxon, and scattered distributions provide justification for listing as Near Threatened in the Northern Territory, Rare in Victoria and Rare in South Australia.

Common names: Antler Zigzag Lily, Club-fruit Lily, Sand Lily.

Etymology: The specific epithet is from the Greek *likros* (antler) and *-ota* (resemblance), in reference to the barbellate, antler-like caruncle on the seeds.

Affinities: *Corynotheca licrota* may be most closely related to *C. lateriflora*, differing in having fibrous (*vs* fleshy-fibrous) roots, persistent (*vs* dry at anthesis) basal leaves 2.5–4.1(–9) (*vs* 0.6–2.2) mm wide, 5–17 (*vs* 4–7) nodes per racemule, racemules 0.4–1.3 (*vs* 0.1–0.6) mm diam., perianth 4.3–6.0 (*vs* 6.5–8.0) mm long and seeds 3.0–4.3 (*vs* 5.0–6.8) mm long with colliculate (*vs* folded) caruncle lobes.

Notes: While MEL 106891 is simply labelled with the location 'Murray', and MEL 107232 with 'Sandridges on the River Murray', duplicate sheets of Mueller's collections often had much-reduced labels and the material is very similar to the holotype, so they are considered possible isotype material.

Henderson (1987) recorded 2–6 flowers per node, but no specimens were seen matching this observation, most being solitary, and just a few flowers were paired. This may be a carry-over from previous literature based on a misidentified *Caesia* collection. This relatively rare species is not often seen flowering. Observations in Victoria suggest that flowers open late in the day (Eichler 2018). It has been observed with open flowers at various times

of the day in South Australia (D. Duval, pers. comm.) and flowering is probably influenced by specific daily conditions, especially heat, so they may close early the following day unless conditions are favourable. The seasonality of flowering appears to be heavily influenced by rainfall and soil moisture (Eichler 2018).

The leaf bases of this species become fibrous with age, similar to those of *Caesia viscida* Keighery, which has a similar habit to *Corynotheca licrota*.

Corynotheca micrantha (Lindl.) Druce, *Bot. Exch. Club 1916, Suppl.* 2: 616 (1917); *Asparagus micranthus* Lindl., *Edwards's Bot. Reg.: Sketch Veg. Swan R. Colony* lviii (1840), *non* Siebold & Zucc. ex Baker (1875); *Corynotheca micrantha* (Lindl.) J.F.Macbride, *Contr. Gray Herb*. 56: 3 (1918), *nom. superfl.*

Type: Swan River, Western Australia, 1839, *J. Drummond s.n.* (holo: CGE, *n.v.*, photos at BRI, PERTH).

Thysanotus micranthus Endl. in Lehmann, J.G.C. (ed.), *Pl. Preiss.* 2(1): 36 (1846).

Type: In arenosis supra oppidulum Perth, Western Australia, 28 November 1839, *L. Preiss* [*Plantae Preissianae* No. 1576] (lectotype here designated: LD 1067334*; isolecto: MEL 107503).

Residual syntype: Wellington district, Western Australia, December 1839, *L. Preiss* [*Plantae Preissianae* No. 1566] (syn: LD 1056262*; MEL 107502).

Thysanotus micranthus var. *minor* Endl. in Lehmann, J.G.C. (ed.), *Pl. Preiss.* 2(1): 36 (1846).

Type: In arenosis supra oppidulum Perth, Western Australia, 28 November 1839, *L. Preiss* [*Plantae Preissianae* No. 1576] (holo: LD 1067334*; iso: MEL 107503).

Thysanotus micranthus var. *major* Endl. in Lehmann, J.G.C. (ed.), *Pl. Preiss.* 2(1): 36 (1846).

Type: Wellington district, Western Australia, December 1839, *L. Preiss* [*Plantae Preissianae* No. 1566] (holo: LD 1056262*; iso: MEL 107034, MEL 107502, P 00852456*, S 06-3249*).

Tufted, tangled, rhizomatous *perennial*, glabrous. *Roots* many, at least 50 mm long, fleshy-fibrous, sand-binding. *Stems* clonal, 10–20 cm long and 1.5–2.4 mm diam. *Leaves* few, linear-subulate, 28–105 mm long, 0.6–1.6 mm wide, flat to involute, reducing rapidly to bracts upwards, all usually senesced by anthesis. *Inflorescence* perennating, irregularly paniculate, interrupted, evenly diffuse, 30–80 cm long, dark green; peduncle ascending, subterranean at base; major branches ascending to spreading to decumbent; lowest branch 1–8 cm from rhizome; panicle branches dichotomously divaricate, each node divaricate at 80–150°; racemules with axis tortuous, 12–40 mm long, with 2–4 nodes, each node divergent at 130–180°, finely ribbed, but otherwise smooth; internodes 4–12 mm long, 0.3–0.6 mm wide, straight to gently curving; flowers solitary in branch axils, most developing; lower bracts linear-subulate, 9–35 mm long, acuminate; uppermost bracts obovate to ±triangular, 0.7–2.6 mm long; pedicels 1.2–2.9 mm long. *Perianth* 2.8–4.5 mm long, segments connate for *c.* 0.4 mm, spirally twisting after anthesis, deciduous. *Sepals* narrowly oblong, 2.6–4.4 mm long, 1.0–1.1 mm wide, apex apiculate, with a minute appendage *c.* 0.1 mm long, margins white, median band darker, pink to purplish. *Petals* narrowly oblong, 2.5–4.3 mm long, 0.9–1.0 mm wide, acute, margins white to cream, median band slightly darker. *Filaments* held erect, straight or slightly incurving, subequal, 1.7–2.1 mm long, somewhat dilated, minutely papillose, white; anthers 0.4–0.8 mm long. *Style* filiform, to 2.0 mm long, equalling or exceeding stamens. *Capsule* nodding, obpyriform, 3.5–5.5 mm long, *c.* 1.5 mm wide, brown, slightly wrinkled. *Seed* 1(2) per fruit, 2.3–3.4 mm long, *c.* 1.2 mm wide, glossy black to iridescent, longitudinally striate; caruncle conical distally, the lobes fused. *2n* = 42 (G.J. Keighery, *Feddes Repert*. 95: 527 (1984); *Keighery 2074*) (Figures 3b, 18).

Diagnostic characters: Basal leaves 28–105 mm long, inflorescence branches flexible, racemules 12–40 mm long, internodes diverging at 130–180°, slender, ±flexible, straight to diverging, not pungent, 0.3–0.6 mm wide, perianth 2.8–4.5 mm long, seeds 2.3–3.4 mm long.

Selected specimens examined: WESTERN AUSTRALIA: Lake Mealup, 25 km W of Pinjarra, 20 Nov. 2004, *K.E. Creed 173* (CANB, PERTH); 14.6 km E along Kondinin–Hyden Road from Kondinin, 5 Apr. 2001, *R. Davis 9694* (PERTH); Lot 505 Hungerford Avenue, Halls Head, Dec. 2001, *P. Foreman 360* (PERTH); Kingsway Sporting Complex, City of Wanneroo, 22 Nov. 2005, *G. Guerin & G. Busby GG 155* (CANB, PERTH); Western Titanium leases, 8 km S of Eneabba, 18 Sept. 1977, *R.J. Hnatiuk 771228* (PERTH); *c.* 5 km W of Brand Highway Beermullah West Road, 24 Nov. 1995, *B.J. Keighery 2115* (PERTH); Bayswater, Lower Swan River, 27 Nov. 1897, *A. Morrison 7330* (BRI); 'Sub' [Subiaco], 19 Jan. 1901, *A. Morrison s.n.* (BRI AQ053436); 'C' [?Cannington], 26 Dec. 1901, *A. Morrison s.n.* (BRI AQ053435); Claremont, 6 Nov. 1907, *A. Morrison s.n.* (CANB 00594975); Mogumber, Moore River, 14 Nov. 1906, *A. Morrison 16225* (PERTH); Marchagee Nature Reserve, Midlands Highway, S of Coorow, 27 July 1999, *F. Obbens 133/99* (PERTH).

Fig. 18. *Corynotheca micrantha*. A, B. Habit. C. Flowering branches. D, E. Flowers. F. Fly visiting flower. Vouchers: A: Gnangarra (not vouchered); B, C, E: Kings Park, Perth (not vouchered); D: Mount Lawley, Perth, *K.R. Thiele 3127* (PERTH); F: Beeliar Bushland (not vouchered). Photographs by A: R. Cumming; B: R.L. Barrett; C, E: E. Pin Tay; D: K. Thiele; F: M. Brundrett.

Distribution: From Eneabba south to Dunsborough and inland to Kondinin in Western Australia, but mostly restricted to the coastal plain and adjacent sand lenses along the Darling Range (Figure 8B).

Habitat: Grows on white, grey and yellow sands, sometimes over limestone or laterite, commonly in *Banksia* woodland with *Acacia pulchella*, *Allocasuarina huegelii*, *A. humilis*, *Austrostipa flavescens*, *Banksia attenuata*, *B. burdettii*, *B. prionotes*, *B. sessilis*, *Burchardia congesta*, *Caesia micrantha*, *Corymbia calophylla*, *Daviesia triflora*, *Eremaea pauciflora*, *Eucalyptus foecunda*, *E. gomphocephala*, *Hakea prostrata*, *H. trifurcata*, *Jacksonia* spp., *Lepidosperma calcicola*, *Macarthuria australis*, *Mesomelaena pseudostygia*, *Synaphea spinulosa*, *Xanthorrhoea brunonis*, and *X. preissii*.

Phenology: Flowers mostly June–January.

Conservation status: *Corynotheca micrantha* is relatively widespread, locally common and is not currently considered threatened, though its habitat on the Swan Coastal Plain has been significantly reduced by urban and agricultural development.

Common names: Hexagon Zigzag Lily, Sand Lily.

Etymology: The specific epithet is from the Greek *micro-* (little, small) and *anthos* (flower), in reference to the small flowers of this species relative to related genera.

Affinities: *Corynotheca micrantha* may be most closely related to *C. elongata*, which has a largely overlapping range, differing in the longer basal leaves 28–105 (*vs* 5–34) mm long, shorter racemules 12–40 (*vs* 37–78) mm long and fewer nodes 2–4 (*vs* 4–8) per racemule.

Corynotheca acanthoclada may also be closely related to *C. micrantha*, most readily distinguished by the relatively short racemules that are rigid, with pungent apices.

Notes: While previously included under *C. micrantha*, we consider the varieties recognised by Henderson (1987) to be equally as distinct as other species recognised in the genus based on a morphological assessment of taxa.

Macbride (1918) independently made the combination *Corynotheca micrantha* (Lindl.) J.F.Macbride, *Contr. Gray Herb*. 56: 3 (1918), but this is superfluous as it was preceded by Druce (1917).

Endlicher (1846) named *Thysanotus micranthus* with two varieties, var. *minor* Endl. and var. *major* Endl. Specimens were only cited under the varieties, so one must be a nomenclatural synonym of the typical variety. As var. *major* was noted to be "An species propria?", it is here interpreted that Endlicher considered var. *minor* to be the typical variety, so a lectotype is designated here to reflect this intent.The lectotype is a good specimen from Lehmann's herbarium (now in LD), while the isolectotype is from Sonder's herbarium (now in MEL).

This species shows a remarkable superficial similarity to *Drimia intricata* (Baker) J.C.Manning & Goldblatt, a bulbous Asparagaceae from southern Africa that Thunberg proposed to name '*Asparagus micranthus*' on herbarium sheets, but apparently did not formally publish. Jessop (1977) listed '*Asparagus micranthus* Thunb.' as a synonym of *Schizobasis intricata* (Baker) Baker (= *Drimia intricata*), but did not validate the name in doing so.

Corynotheca panda (R.J.F.Hend.) R.L.Barrett & T.Macfarlane, *comb. et stat. nov*.

Basionym: *Corynotheca micrantha* var. *panda* R.J.F.Hend., *Fl. Austral.* 45: 475, 303, fig. 70g (1987).

Type: junction of Martin Creek with Fitzgerald River, Reserve 24048, Western Australia, 19 December 1970, *A.S. George 10576* (holo: PERTH 01221515; iso: PERTH 01221523).

Tufted, tangled, rhizomatous *perennial*, glabrous. *Roots* many, 60–170 mm long, fleshy-fibrous, sand-binding. *Stems* short, to 15 mm long and 5 mm diam. *Leaves* few, linear-subulate, to 45–180 mm long, 0.7–1.6 mm wide, flat, reducing rapidly to bracts upwards, all usually senesced by anthesis. *Inflorescence* perennating, interrupted, subunits reduced to elongated simple or few-branched branches, 30–50 cm long, dark to olive green; peduncle erect to ascending to decumbent, subterranean at base; major branches spreading to decumbent; lowest branch 11–32 cm from rhizome; panicle branches diverging, each node diverging at (90–)130–170°; racemules with axis irregularly curving to tortuous, 18–106 mm long, with (2–)5–8 nodes, each node divergent at 140–180°, finely ribbed, but otherwise smooth or crenulate; internodes 8–19 mm long, 0.3–0.7 mm wide, ±straight to evenly curving; flowers solitary or paired in branch axils, few–many developing; lower bracts linear-subulate, 7–25 mm long, acuminate; uppermost bracts narrowly ±triangular, 1.0–2.1 mm long; pedicels 1.3–2.9(–3.5) mm long. *Perianth* 3.5–4.6 mm long, segments connate for *c*. 0.7 mm, spirally twisting after anthesis, deciduous. *Sepals* narrowly oblong, 3.3–4.5 mm long, 0.7–1.2 mm wide, apex apiculate, with a minute appendage *c*. 0.5 mm long, white at the base, grading to pink to purplish to brown, median band slightly darker. *Petals* narrowly oblong, 3.2–4.3 mm long, 0.6–0.8 mm wide, acute, white to cream, median band slightly darker. *Filaments* slightly spreading, straight or slightly incurving, subequal, 1.7–2.0 mm long, slightly dilated, minutely papillose, white; anthers 0.5–0.6 mm long. *Style* filiform, to 1.8 mm long, slightly exceeding stamens. *Capsule* spreading to antrorse, obpyriform, 3.8–5.2 mm long, 1.6–1.9 mm wide, brown, slightly wrinkled. *Seed* 1 per fruit, 2.8–3.3 mm long, *c*. 1.6 mm wide, glossy black to iridescent, longitudinally striate; caruncle conical distally, the lobes fused. (Figures 4b, 19)

Diagnostic characters: Basal leaves 45–180 mm long, racemules with (2–)5–8 nodes, internodes diverging at 140–180°, internodes 8–19 mm long, 0.3–0.7 mm diam., ±straight to evenly curving, seeds 2.8–3.3 mm long.

Selected specimens examined: WESTERN AUSTRALIA: Walpole Nornalup National Park, 13 Dec. 1988, *A.R. Annels 532* (PERTH); Lort River crossing, *c*. 70 km W of Esperance along road to Ravensthorpe, 8 Jan. 1979, *B. Barnsley 409* (CBG); Taylor Island, Recherche Archipelago, 5 Jan. 2011, *S. Barrett & E. Adams 1929* (PERTH); near Israelite Bay, Dec. 1884, *S.T. Brooks s.n.* (MEL 107051); Cape Arid National Park camp ground on the western side of the Thomas River, 8 Nov. 2006, *G. Byrne 2481* (PERTH); Jorndee Creek campsite, Condingup, 10 Apr. 2007, *G. Byrne 2621* (PERTH); Chillilup Pool on Pallinup River, 14 Jan. 1979, *M.D. Crisp 5148* (CBG); 400 m W of Meerup River, 50 m S of track, 27 Feb. 1997, *C. Day & P. Ellery P 75.3* (PERTH); Knoll overlooking ocean S of Elephant Rock carpark, William Bay National Park (Plot: wil5), 27 Nov. 1990, *N. Gibson & M. Lyons 853* (PERTH); William Bay National Park, dunes above Madfish Bay carpark, 18 Nov. 1990, *B.G. Hammersley 489* (PERTH); Blackwood River, *M. McHard s.n.* (MEL 107052); Gold Holes, Chester Pass road, Stirling Ranges, 17 Nov. 1982, *G.J. Keighery 5635* (PERTH); Pallinup River, Chillinup, 20 Apr. 2000, *P.D. Moir 202* (PERTH); East of Hopetoun in first ten miles [16 km] of track, *M.E. Phillips s.n.* (CBG 11374); Eastern slope of Mount Arid, in saddle between saddle and large dome to East, 23 Nov. 1985, *A.N. Rodd 5144* (BRI, CANB, MEL, NSW, PERTH); Helms Arboretum Bushland, 30 Mar. 2011, *C.D. Turley & R.M. Hoggart 11/303-11* (CANB, PERTH); Lot 14 View Range Road, Tenterden, 75 m S of shed, 28 Dec. 2005, *J.E. Wajon 1426* (PERTH).

Fig. 19. *Corynotheca panda*. A. Habit. B. Flowering branches. C. Flowering branchlet. D. Fruit. E. habitat. Vouchers: A, E: Cape Arid National Park, *G. Byrne 2481* (PERTH); B, D, F: Seal Creek, *G. Byrne 2621* (PERTH); C: Torbay Inlet, Albany, *R. Davis 12989* (PERTH). Photographs by G. Byrne (A, B, D–F); R. Davis (C).

Distribution: Scattered along the south coast of Western Australia between the Blackwood River and Cape Arid, extending inland to the Stirling Ranges (Fig. 7).

Habitat: Grows on sandy or sandy clay soils, over siltstone or granite, in heath or open woodland with *Acacia saligna*, *Allocasuarina thuyoides*, *Comesperma flavum*, *Conospermum teretifolium*, *Eucalyptus rudis*, *E. tetraptera*, *Hibbertia oligantha*, *H. psilocarpa*, *Lechenaultia tubiflora*, *Leptospermum* sp., *Leucopogon* sp. Coujinup (M.A.Burgman 1085), *Lysinema ciliatum*, *Melaleuca pulchella*, *M. striata*, *Ornduffia parnassifolia*, *Schoenus caespititius*, *Stirlingia tenuifolia*, *Stylidium repens*, *Velleia trinervis* and *Xanthorrhoea platyphylla*.

Phenology: Flowers mostly between October–December.

Conservation status: *Corynotheca panda* is widespread and is not currently considered threatened.

Common name: Panda Zigzag Lily.

Etymology: The specific epithet is from the Latin *pandus* (bent), in reference to the curving racemule axes.

Affinities: *Corynotheca panda* appears to be most closely related to *C. elongata*, differing in the basal leaves 45–180 (*vs* 5–34) mm long, racemules diverging at 140–180° (*vs* diverging or straight (160–)170–180°), 0.3–0.7 (*vs* 0.2–0.5) mm diam., ±straight to evenly curving (*vs* ±straight) and seeds 2.8–3.3 (*vs* 1.8–2.7) mm long.

Notes: Henderson (1987) thought that this taxon may merge with *C. elongata*, and their geographical ranges do approach each other, but morphological intergradation has not been observed, and based on current collections, their ranges do not actually overlap.

Corynotheca pungens R.J.F.Hend., *Fl. Austral.* 45: 475, 304, figs 70k, 96h, i (1987).

Type: Gascoyne R., at crossing by North West Coastal Hwy, *c.* 15 km by road ENE of Carnarvon, Western Australia, 31 August 1977, *E.N.S. Jackson 3092* (holo: AD, *n.v.*; iso: BRI AQ0424269 [2 sheets], NSW, PERTH 01221485, PERTH 01221493, PERTH 01221507).

Corynotheca lateriflora var. *laevisperma auct. non* Gauba: E.Gauba, *Vict. Nat.* 65: 111, 113 (1948), *p.p.*

Tufted, tangled, rhizomatous *perennial*, glabrous. *Roots* many, at least 50 mm long, fleshy-fibrous, sand-binding. *Stems* not seen. *Leaves* single–many, mostly cauline, clustered at nodes, linear-subulate, to 40–110 mm long, 0.5–2 mm wide, flat, margins sometimes with scabrid hairs, reducing to bracts on upper branchlets, persistent. *Inflorescence* perennating, irregularly paniculate, 50–100 cm long, dark green; peduncle ascending to decumbent, subterranean at base; major branches decumbent; lowest branch 5–20 cm from rhizome; panicle branches dichotomously divaricate, each node divaricate at 90–150°; racemules with axis not twisted, 30–140(–300) mm long, with 5–21 nodes, each node divergent at 170–180°, finely ribbed, but otherwise smooth; internodes 3–14(–30) mm long, 0.6–1.1 mm wide, ±straight; flowers solitary in branch axils, ?few–most developing; lower bracts linear-subulate, 17–100 mm long, acute, pungent; uppermost bracts ovate-attenuate, 0.8–5.2 mm long; pedicels 0.9–1.7(–3.0) mm long. *Perianth* 2.7–6.1 mm long, segments connate for *c.* 0.5 mm, spirally twisting after anthesis, deciduous. *Sepals* narrowly elliptic, 2.6–5.8 mm long, 1.1–1.2 mm wide, apex apiculate, with a minute appendage *c.* 0.2 mm long, margins white, median band darker, pink to purplish to brown. *Petals* narrowly elliptic to obovate, 2.5–5.6 mm long, 0.9–1.0 mm wide, emarginate, white to cream, median band sometimes darker. *Filaments* erect to spreading, incurving, straight (i.e. not kinked), subequal to unequal 2.1–2.6 mm long, slightly dilated, minutely papillose, yellow; anthers 0.7–1.2 mm long. *Style* filiform, to 3.2 mm long, exceeding stamens. *Capsule* ascending to pendulous, clavate to obpyriform, 3.5–5.5 mm long, *c.* 1.7 mm wide, brown, slightly wrinkled. *Seeds* 1 or 2 per fruit, 2.7–2.9 mm long, *c.* 1.2 mm wide, glossy black to iridescent, (smooth or) longitudinally striate; caruncle conical distally, the lobes ±fused (Figures 5a, 20).

Diagnostic characters: Mature basal leaves mostly dry at anthesis but with mature cauline leaves not reduced to bracts, persistent, and clustered in major axils, 40–110 mm long, upper bract apices stiff, ±pungent, racemules 0.6–1.1 mm diam., caruncle lobes on seeds fused.

Selected specimens examined: WESTERN AUSTRALIA: 12 km SW of Onslow, 29 Aug. 2010, *J. Alford JJA 2009/3* (PERTH); Turee Creek Sandplain, S of Turee Creek Station, N Gascoyne, 27 Oct. 2000, *S. Black s.n.* (MEL, PERTH); Near sea wall, Port Hedland, 11 May 1941, *N.T. Burbidge 625* (PERTH); Ashburton River, 1883, *H.S. Carey s.n.* (MEL 107233); near Roebourne, *H.S. Carey s.n.* (MEL 107072); Strelly River, Aug.-Sept. 1907, *J.B. Cleland s.n.* (PERTH 1968343); Finucane Island, 15 Jul. 1981, *G. Craig 272* (PERTH); near Yule River, 1878, *J. Forrest s.n.* (MEL 107063); Sherlock River, 1878, *J. Forrest s.n.* (MEL 107069); Tuckanarra Creek, 13 Oct. 1945, *C.A. Gardner 7842* (PERTH); E of Learmonth Airfield, 8 Sept. 1970, *A.S. George 10346* (CANB, MEL, PERTH); Tent Island Nature Reserve, 29 July 2015, *N. Godfrey NG 1/15* (PERTH); Monkey Mia, Shark Bay, 30 Aug. 1989, *G.J. Keighery 10444* (CANB, PERTH); Mardathuna Station on main track to Binthalya

Homestead 2.5 km NNE of Yoweroo Well, 18 Aug. 1994, *G.J. Keighery & N. Gibson 1573* (CANB, PERTH); Old Onslow, 22 Aug. 2006, *G.J. Keighery & B.J. Keighery 762* (MEL, PERTH); coastal strip 5 km W of Urala Homestead, 30 km SE of Onslow, 14 Aug. 1992, *V. Long VL 439* (PERTH); 14.6 km NW of Wodgina Mining Centre, 35.2 SW of Indee Station Homestead and 37 km S of Wallareenya Station Homestead, 21 Mar. 2004, *M. Maier BES 598* (CANB, PERTH); 10–15 km E of Homestead in Giralia Station S of Exmouth Gulf, 13 June 2004, *K. McCreery GIR 04-13* (CANB, PERTH); *c.* 15 km NNW of De Grey Homestead on W side of De Grey River, 26 Sept. 1994, *A.A. Mitchell 3782* (PERTH); Onslow, Mouth of Ashburton River, 26 Sept. 1905, *A. Morrison s.n.* (BRI AQ053433); Banks of Ashburton River at Minderoo, 8 Oct. 1905, *A. Morrison 15163* (PERTH); Murchison River [presumably headwaters], *A.F. Oldfield s.n.* (MEL 107270, MEL 107070); 11 miles S of Carnarvon, 12 July 1959, *R.D. Royce 5854* (PERTH); Mardathuna Road, Kennedy Range National Park, 8 July 2015, *K.R. Thiele 5223* (PERTH); Peron Peninsula, Shark Bay, 2 Nov. 1989, *M.E. Trudgen 7503* (PERTH); 3.6 km NE of Red Hill, 5.6 km SW of Paruwarranha Hill, 25.5 km E of Whim Creek, Mundabullangana Station, 20 Aug. 2004, *S. van Leeuwen et al. PBS 5347* (PERTH).

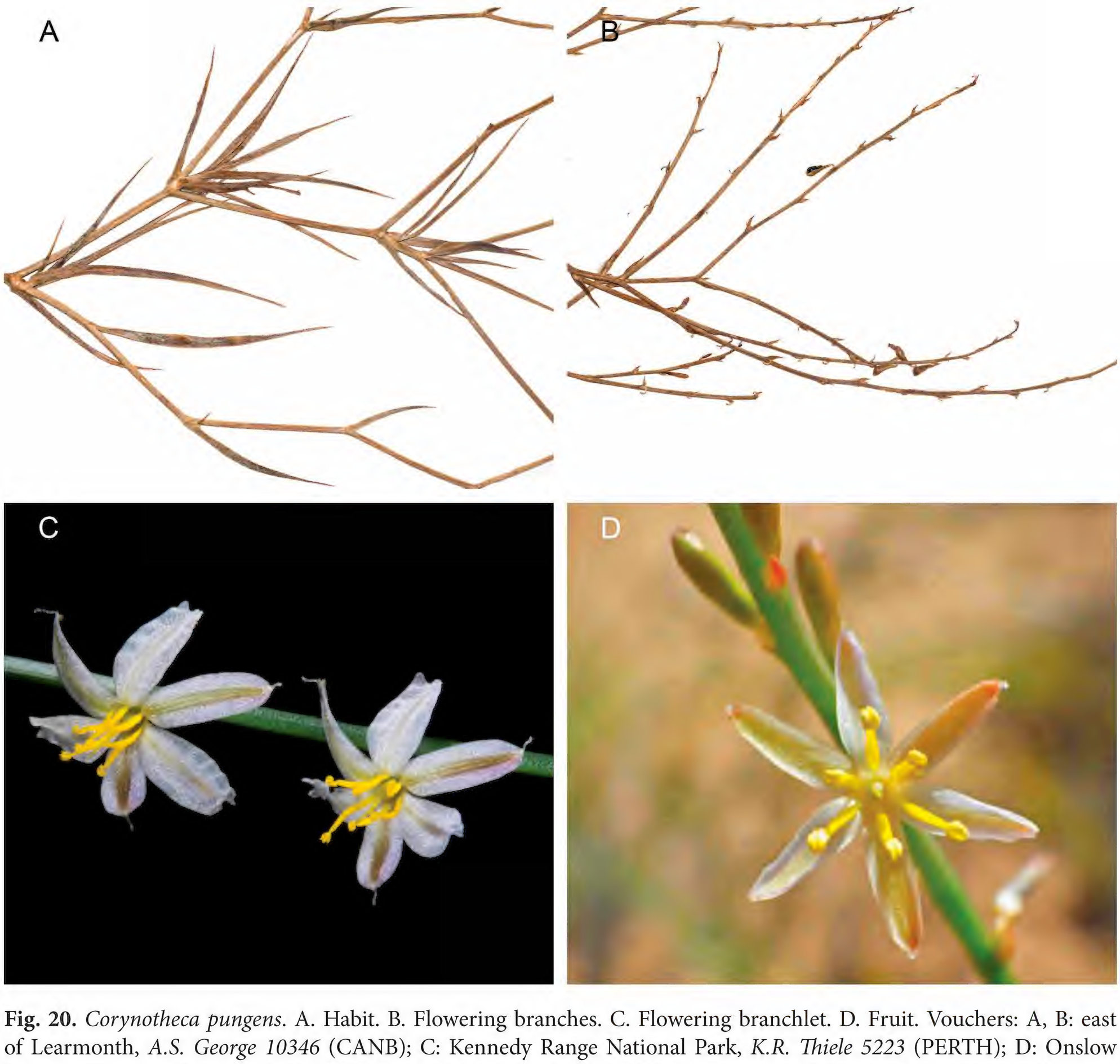

Fig. 20. *Corynotheca pungens*. A. Habit. B. Flowering branches. C. Flowering branchlet. D. Fruit. Vouchers: A, B: east of Learmonth, *A.S. George 10346* (CANB); C: Kennedy Range National Park, *K.R. Thiele 5223* (PERTH); D: Onslow (not vouchered). Photographs by R.L. Barrett (A, B); K.R. Thiele (C); Department of Biodiversity, Conservation and Attractions (D).

Distribution: From Port Headland south to Shark Bay, inland to Newman in Western Australia (Fig. 7).

Habitat: Grows on sandy dunes or flats and sandy clay or loam soils, in river channels, or sometimes on beach sand, in shrubland, tussock grassland or hummock grassland with *Acacia coriacea*, *A. murrayana*, *A. sclerosperma*, *A. tetragonophylla*, *A. trachycarpa*, *Atalaya hemiglauca*, *Brachycome latisquamea*, *Chorizema racemosum*, *Eremophila subfloccosa*, *Eucalyptus camaldulensis* subsp. *refulgens*, *Eulalia aurea*, *Exocarpos*

sparteus, *Grevillea gordoniana*, *Hakea lorea* subsp. *lorea*, *Quoya loxocarpa*, *Rhagodia preissii*, *Rhynchosia minima*, *Santalum lanceolatum*, *Triodia basedowii*, and *T. epactia*.

Phenology: Flowers mostly June–August.

Conservation status: *Corynotheca pungens* is widespread and is not currently considered threatened.

Common name: Spiny Sand Lily.

Etymology: The specific epithet is from the Latin *pungens* (sharp, piercing), in reference to the sharp lower bract apices.

Affinities: *Corynotheca pungens* is a distinctive species of uncertain affinity, but it may be most closely related to *C. licrota* with which it shares long, persistent leaves and long racemules with many nodes that are ±straight. The bracts of *C. licrota* are acuminate and sharp, but not pungent as in *C. pungens*. *Corynotheca pungens* differs in having a spreading (*vs* erect) habit, fleshy-fibrous (*vs* fibrous) roots, mostly cauline (*vs* mostly basal) leaves, slender leaves 0.5–2 (*vs* 2.5–4.1(–9)) mm wide, more divergent panicle branches 90–150° (*vs* 130–160°), smaller seeds 2.7–2.9 (*vs* 3.0–4.3) mm long with fused, colliculate (*vs* free and folded) caruncle lobes.

Notes: Gauba (1948) included a few specimens of this taxon under his concept of the taxon here recognised as *C. licrota* (treated there as *Corynotheca lateriflora* var. *laevisperma*).

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References

Angiosperm Phylogeny Group (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181: 1–20. http://dx.doi.org/10.1111/boj.12385

Bailey FM (1913) *Comprehensive catalogue of Queensland plants*. (H.J. Diddams and Co.: Brisbane)

Baker J (1876) Revision of the genera and species of Anthericeae and Eriospermeae. *Journal of the Linnean Society of London, Botany* 15: 253–363.

Barrett MD (2018) Three new species of Asparagales from the Kimberley region of Western Australia. *Telopea* 21: 25–37. http://dx.doi.org/10.7751/telopea11463

Barrett RL, Barrett MD (2015) Twenty-seven new species of vascular plants from Western Australia. *Nuytsia* 26: 21–87. https://florabase.dpaw.wa.gov.au/science/nuytsia/730.pdf

Barrett RL, Dixon KW (2001) A revision of the genus *Calectasia* (Calectasiaceae) with eight new species described from south-west Western Australia. *Nuytsia* 13: 411–448. https://www.biodiversitylibrary.org/page/53424718

Barrett RL, Pin Tay E (2016) *Perth plants. A field guide to the bushland and coastal flora of Kings Park and Bold Park, Perth*. Second edn. (CSIRO Publishing: Melbourne)

Barrett RL, Wilson KL (2012) A review of the genus *Lepidosperma* (Cyperaceae: Schoeneae). *Australian Systematic Botany* 25: 225–294. https://doi.org/10.1071/SB11037

Barrett RL, Wilson KL, Bruhl JJ (2020) Reinstatement and revision of the genus *Chaetospora* (Cyperaceae: Schoeneae). *Telopea* 23: 95–112. https://dx.doi.org/10.7751/telopea14345

Bennett EM, Dundas P (1988) *The bushland plants of Kings Park Western Australia*. (Kings Park Board: Perth, WA)

Bentham G (1878) *Flora Australiensis: A description of the plants of the Australian Territory. Vol. VII. Roxburghiaceae to Filices*. (Lovell Reeve: London) https://doi.org/10.5962/bhl.title.141

Black JM (1922) *Flora of South Australia Part 1. Cyatheaceae – Orchidaceae*. 1st edn. (Government Printer: Adelaide)

Black JM (1943) *Flora of South Australia Part 1*. 2nd edn. (Government Printer: Adelaide)

Boatwright JS, Manning JC (2010) *Caesia sabulosa* (Hemerocallidaceae), a new species from the Greater Cape Region of South Africa. *South African Journal of Botany* 76: 524–529. https://doi.org/10.1016/j.sajb.2010.04.007

Brown R (1810) *Prodromus florae Novae-Hollandiae et insulae van-Diemen*. (Taylor: London)

Chase MW, de Bruijn AY, Cox AV, Reeves G, Rudall PJ, Johnson MAT, Eguiarte LE (2000) Phylogenetics of Asphodelaceae (Asparagales): An analysis of plastid *rbcL* and *trnL-F* DNA sequences. *Annals of Botany* 86: 935–951. http://dx.doi.org/10.1006/anbo.2000.1262

Chase MW, Reveal JL, Fay MF (2009) A subfamilial classification for the expanded asparagalean families Amaryllidaceae, Asparagaceae and Xanthorrhoeaceae. *Botanical Journal of the Linnean Society* 161: 132–136. http://dx.doi.org/10.1111/j.1095-8339.2009.00999.x

Chase MW, Rudall PJ, Conran JG (1996) New circumscriptions and a new family of Asparagoid lilies: genera formerly included in Anthericaceae. *Kew Bulletin* 51: 667–680. http://dx.doi.org/10.2307/4119721

Chen S, Kim D-K, Chase MW, Kim J-H (2013) Networks in a large-scale phylogenetic analysis: reconstructing evolutionary history of Asparagales (Lilianae) based on four plastid genes. *PLoS ONE* 8: e59472. http://dx.doi.org/10.1371/journal.pone.0059472

Clifford HT, Conran JG (1998) Johnsoniaceae. Pp. 336–340 in K Kubitzki (Ed.) *The Families and Genera of Vascular Plants. Volume III. Flowering Plants. Monocotyledons. Lilianae (except Orchidaceae)*. (Springer-Verlag: Berlin) http://dx.doi.org/10.1007/978-3-662-03533-7_39

Clifford HT, Conran JG, Thongpukdee A (1992) Australian lilies: native and naturalised species. *Australian Plants* 16: 335–377.

Clifford HT, Henderson RJF, Conran JG (1998) Hemerocallidaceae. Pp. 245–253 in K Kubitzki (Ed.) *The Families and Genera of Vascular Plants. Volume III. Flowering Plants. Monocotyledons. Lilianae (except Orchidaceae)*. (Springer -Verlag: Berlin) http://dx.doi.org/10.1007/978-3-662-03533-7_32

Conran JG, Walsh NG (1994) Liliaceae. Pp. 637–686 in NG Walsh and TJ Entwisle (Eds) *Flora of Victoria Volume 2. Ferns and allied plants, conifers and monocotyledons*. (Inkata Press: Melbourne)

Cunningham GM, Mulham WE, Milthorpe PL, Leigh JH (1981) *Plants of Western New South Wales*. (N.S.W. Government Printing Office: Sydney)

Devey DS, Leitch IJ, Rudall PJ, Pires JC, Pillon Y, Chase MW (2006) Systematics of Xanthorrhoeaceae sensu lato, with emphasis on *Bulbine*. Pp. 345–351 in JT Columbus, EA Friar, JM Porter, LM Prince and MG Simpson (Eds) *Monocots: comparative biology and evolution (excluding Poales). Aliso 22*. (Rancho Santa Ana Botanic Garden: Claremont, California)

Druce GC (1917) Nomenclatural notes; chiefly African and Australian. *The Botanical Exchange Club and Society of the British Isles* Report for 1916: 601–653.

Eichler H (1965) *Supplement to J.M. Black's Flora of South Australia (second edn, 1943–1957)*. pp. 82–83. (Government Printer: Adelaide, Hawes)

Eichler J (2018) Flowering of the sand lily *Corynotheca licrota* R.J.F.Hend.: observations in Victoria. *Victorian Naturalist* 135: 23–24.

Endlicher SFL (1846) Liliaceae. Pp. 33–39 in JGC Lehmann. *Plantae Preissianae sive enumeratio plantarum, quas in Australasia Occidentali et Meridionali-occidentale annis 1838–1841 collegit Ludovicus Preiss, Ph. Dr. Vol. 2(1)*. (J.A. Meissner: Hamburg)

Fay MF, Rudall PJ, Sullivan S, Stobart KL, de Bruijn AY, Reeves G, Qamaruz-Zaman F, Hong W-P, Joseph J, Hahn WJ, Conran JG, Chase MW (2000) Phylogenetic studies of Asparagales based on four plastid DNA regions. Pp. 360–371 in KL Wilson and DA Morrison (Eds) *Monocots. Systematics and evolution*. (CSIRO Publishing: Collingwood)

Furness CA, Conran JG, Gregory T, Rudall PJ (2014) The trichotomosulcate asparagoids: pollen morphology of Hemerocallidaceae in relation to systematics and pollination biology. *Australian Systematic Botany* 26: 393–407. https://doi.org/10.1071/SB13046

Gauba E (1948) Contributions to the Flora of South Australia—1. *Victorian Naturalist* 65: 110–113.

Givnish TJ, Zuluaga A, Spalink D, Soto Gomez M, Lam VKY, Saarela JM, Sass C, Iles WJD, Lima deSousa DJ, Leebens-Mack JH, Pires JC, Zomlefer WB, Gandolfo MA, Davis JI, Stevenson DW, dePamphilis CW, Specht CD, Graham SW, Barrett CF, Ané C (2018) Monocot plastid phylogenomics, timeline, net rates of species diversification, the power of multi-gene analyses, and a functional model for the origin of monocots. *American Journal of Botany* 105: 1888–1910. https://doi.org/10.1002/ajb2.1178

Henderson RJF (1987) *Corynotheca*. Pp. 299–306; 473–475 in AS George (Ed.) *Flora of Australia*. (Australian Government Publishing Service: Canberra)

Jessop JP (1977) Studies in the bulbous Liliaceae in South Africa: 7. The taxonomy of *Drimia* and certain allied genera. *Journal of South African Botany* 43: 265–319.

Jessop JP (1981) Liliaceae. Pp. 419–424 in JP Jessop (Ed.) *Flora of Central Australia*. (Australian Systematic Botany Society / A.H. & A.W. Reed Pty Ltd: Sydney)

Jessop JPP (1986) Liliaceae. Pp. 1742–1775 in JPP Jessop and HR Toelken (Eds) *Flora of South Australia. Part IV. Alismataceae-Orchidaceae*. (The Flora and Fauna of South Australia Handbooks Committee: Adelaide)

Kaigongi MM (2020) *Review of botanical name change of trees, shrubs and herbs in Kenya*. Technical Note No. 29. (Kenya Forestry Research Institute: Muguga, Kenya)

Keeble J (2017) *Field guide to Hi Vallee Farm. A revised photographic guide to the kwongan bushland diversity on Don and Joy Williams' property Tootbardie Road, Badgingarra, Western Australia*. (Jolanda Keeble: Perth)

Keighery GJ (1984) Chromosome numbers of Australian Liliaceae. *Feddes Repertorium* 95: 523–532.

Keighery GJ (1987a) *Arnocrinum*. In: AS George (Ed.) *Flora of Australia*. 45: 246–249. (Australian Government Publishing Service: Canberra)

Keighery GJ (1987b) *Laxmannia*. In: AS George (Ed.) *Flora of Australia* 45: 254–264. (Australian Government Publishing Service: Canberra)

Kenneally KF, Edinger DJ, Willing T (1996) *Broome and beyond. Plants and people of the Dampier Peninsula, Kimberley, Western Australia*. (Department of Conservation and Land Management: Perth)

Klopper RR, Smith GF, van Wyk AE (2013) (2129) Proposal to conserve the family name Asphodelaceae (Spermatophyta: Magnoliidae: Asparagales). *Taxon* 62: 402–403. http://dx.doi.org/10.12705/622.17

Macbride JF (1918) Further new or otherwise interesting Liliaceae. *Contributions from the Gray Herbarium of Harvard University* 56: 1–20.

Macfarlane TD (1987) Anthericaceae. Pp. 757–777 in NG Marchant and JR Wheeler (Eds) *Flora of the Perth Region*. (Western Australian Herbarium: Perth)

Macfarlane TD, Conran JG (2015) *Lomandra marginata* (Asparagaceae), a shy-flowering new species from south-western Australia. *Australian Systematic Botany* 27: 421–426. http://dx.doi.org/10.1071/SB14045

Macfarlane TD, Conran JG (2016) Tepal apex trichomes, specialized bud closure structures and their systematic value in Asparagales. *Memoirs of the New York Botanical Garden* 118: 31–42. http://dx.doi.org/10.21135/893275341.012

Macfarlane TD, Conran JG, French CJ (2020a) *Caesia arcuata* (Hemerocallidaceae) from Western Australia, a new rarity with curved inflorescence branches. *Nuytsia* 31: 239–242. https://florabase.dpaw.wa.gov.au/science/nuytsia/984.pdf

Macfarlane TD, French CJ, Conran JG (2020b) A new Fringe Lily from Kalbarri National Park (*Thysanotus kalbarriensis*, Asparagaceae). *Nuytsia* 31: 23–27. https://florabase.dpaw.wa.gov.au/science/nuytsia/940.pdf

Macfarlane TD, Keighery GJ (2015) Two new species of *Tricoryne* (Hemerocallidaceae) from south western Australia. *Australian Systematic Botany* 27: 415–420. http://dx.doi.org/10.1071/SB14046

McCune S, Hardin DW (1993) Anthericaceae. Pp. 86–98 in GJ Harden (Ed.) *Flora of New South Wales*. (University of New South Wales Press: Kensington)

McLay TGB, Bayly MJ (2016) A new family placement for Australian blue squill, *Chamaescilla*: Xanthorrhoeaceae (Hemerocallidoideae), not Asparagaceae. *Phytotaxa* 275: 97–111. http://dx.doi.org/10.11646/phytotaxa.275.2.2

McPherson MA, Fay MF, Chase MW, Graham SW (2004) Parallel loss of a slowly evolving intron from two closely related families in Asparagales. *Systematic Botany* 29: 296–307.

Mueller FJH (1859) *Fragmenta Phytographiae Australiae*. Vol. 1, Part 9. (Melbourne Printers: Melbourne) https://doi.org/10.5962/bhl.title.116758

Mueller FJH von (1870) *Fragmenta Phytographiae Australiae*. Vol. 7, Part 1. (Melbourne Printers: Melbourne) https://www.biodiversitylibrary.org/item/7224#page/69/mode/1up

Nakardbam B (2013) An-ngale makka kah-ngeyyo? part 2 [What's this plant called? part 2] [Blog post, May 15, 2013] https://bininjkunwok.org.au/an-ngale-makka-kah-ngeyyo-part-2/ [Accessed 23 Dec. 2019]

Ochyra R (1990) *Corynotheca*, a remarkable new genus of Funariaceae (Musci) from the Himalayas. *Polish Botanical Studies* 1: 59–65.

Pate JS, Dixon KW (1983) *Tuberous, cormous and bulbous plants*. (University of Western Australia Press: Nedlands)

Raven PH, Miller SE (2020) Here today, gone tomorrow. *Science* 370: 149. https://doi.org/10.1126/science.abf1185

Rudall PJ, Chase MW (1996) Systematics of Xanthorrhoeaceae *sensu lato*: evidence for polyphyly. *Telopea* 6: 629–647. http://dx.doi.org/10.7751/telopea19963028

Rudall PJ, Stobart KL, Hong W-P, Conran JG, Furness CA, Kite GC, Chase MW (2000) Consider the lilies: Systematics of Liliales. Pp. 347–359 in KL Wilson and DA Morrison (Eds) *Monocots. Systematics and evolution*. (CSIRO Publishing: Collingwood)

Rye BL (1992) Anthericaceae. Pp. 994–999 in JR Wheeler (Ed.) *Flora of the Kimberley Region*. (Conservation and Land Management: Perth, WA)

Seberg O, Petersen G (2012) Phylogeny of the Asparagales based on three plastid and two mitochondrial genes. *American Journal of Botany* 99: 875–889. https://doi.org/10.3732/ajb.1100468

Sirisena UM, Conran JG, Macfarlane TD (2016) Formal transfer of *Murchisonia* to *Thysanotus* (Asparagaceae). *Nuytsia* 27: 121–123. https://florabase.dpaw.wa.gov.au/science/nuytsia/790.pdf

Smith NM (1991) Ethnobotanical field notes from the Northern Territory. *Journal of the Adelaide Botanic Gardens* 14: 1–65. https://data.environment.sa.gov.au/Content/Publications/JABG14P001_Smith.pdf

Steele PR, Hertweck KL, Mayfield D, McKain MR, Leebens-Mack JH, Pires JC (2012) Quality and quantity of data recovered from massively parallel sequencing: Examples in Asparagales and Poaceae. *American Journal of Botany* 99: 330–348. http://dx.doi.org/10.3732/ajb.1100491

Stockhouse RE, Wells H (1978) Pollination ecology of *Chlorogalum pomeridianum* (DC.) Kunth.(Liliaceae). *Bulletin of the Southern California Academy of Sciences* 77: 124–129.

Thomson SA, Pyle RL, Ahyong ST, Alonso-Zarazaga M, Ammirati J, Araya JF, *et al.* [184 authors] (2018) Taxonomy based on science is necessary for global conservation. *PLoS Biology* 16: e2005075. https://doi.org/10.1371/journal.pbio.2005075

Wheeler JR, Graham L (2002) Anthericaceae. Pp. 240–251 in JR Wheeler (Ed.) *Flora of the South West. Bunbury, Augusta, Denmark. Flora of Australia Supplementary Series 12*. (Australian Biological Resources Study, Canberra, Conservation and Land Management, Como and University of Western Australia Press: Crawley)

Wurdack KJ, Dorr LJ (2009) The South American genera of Hemerocallidaceae (*Eccremis* and *Pasithea*): two introductions to the New World. *Taxon* 58: 1122–1132.

Western Australian Herbarium (1998–) *FloraBase—the Western Australian Flora*. Department of Biodiversity, Conservation and Attractions. https://florabase.dpaw.wa.gov.au/ [Accessed 11 March 2020]

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Netrostylis, a new genus of Australasian Cyperaceae removed from *Tetraria*

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Abstract

A new genus, *Netrostylis* R.L.Barrett, J.J.Bruhl & K.L.Wilson is described for Australasian species previously known as *Tetraria capillaris* (F.Muell.) J.M.Black (Cyperaceae tribe Schoeneae). The genus is restricted to southern and eastern Australia, and the North Island of New Zealand. Two new combinations are made: *Netrostylis capillaris* (F.Muell.) R.L.Barrett, J.J.Bruhl & K.L.Wilson and *Netrostylis halmaturina* (J.M.Black) R.L.Barrett, J.J.Bruhl & K.L.Wilson. *Netrostylis* is a member of the *Lepidosperma* Labill. Clade.

Keywords: Cyperaceae; *Netrostylis*; *Tetraria*; *Neesenbeckia*; *Machaerina*; Schoeneae; Australia; New Zealand.

Introduction

Recent molecular phylogenetic studies in Cyperaceae have greatly increased our understanding of relationships in the family (Muasya *et al*. 2009; Muasya 2016; Larridon *et. al*. 2018a, 2018b, 2019; Barrett *et al*. 2019, 2021; Semmouri *et al*. 2019; Elliott *et al*. 2021; Larridon *et al*., 2021a, 2021b). This paper provides a new generic name for a segregate group of Australasian species previously included in *Tetraria*, which molecular data have consistently shown to be unrelated to *Tetraria s. str.* Detailed studies of Australasian taxa in the *Lepidosperma* Labill. clade have consistently resolved *Tetraria capillaris* (F.Muell.) J.M.Black sister to the monotypic South African genus *Neesenbeckia* Levyns. These two taxa form a clade sister to the predominantly Australasian genus *Lepidosperma* and these three form a clade sister to the more widespread genus *Machaerina* Vahl. (Larridon *et al*. 2021b). The now established phylogenetic position of *Tetraria capillaris* was first recovered by Slingsby and Verboom (2006) and Verboom (2006). The genus *Tetraria* (*sensu* Levyns 1947, Bruhl 1995 or Goetghebeur 1998) has subsequently been significantly redefined, but remains paraphyletic (Slingsby and Verboom 2006; Verboom 2006; Barrett *et al*. 2012a; Viljoen *et al*. 2013; Elliott and Muasya 2017, 2018, 2019, 2020; Elliott *et al*. 2019, 2021). The nomenclatural changes proposed here are made in advance of a revised global classification of the family Cyperaceae with the aim of circumscribing a monophyletic *Tetraria* (Larridon *et al*. 2017, 2018b, 2021b; Elliott *et al*. 2021).

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Tetraria capillaris has endured a rather tortuous history of generic placement in tribe Schoeneae. Originally described by Hooker (1858) as *Chaetospora capillacea* Hook.f., a name pre-dated by *Chaetospora capillacea* Nees (1834), Mueller (1875) recognised that a new epithet was required and created the name *Chaetospora capillaris* F.Muell. Following this, the generic placement has been in a state of regular flux. Bentham (1878) transferred this species to *Elynanthus* P.Beauv. ex T.Lestib.; Clarke (in Cheeseman, 1906) transferred it to *Cladium* P.Browne; Fernald (1923) placed it in *Mariscus* Scop.; Black (1934) placed it in *Tetraria* where it has generally been accepted (e.g. Moore and Edgar 1970; Rye 1987; Wilson 1993, 1994; Wheeler and Graham 2002); but Koyama (1956) transferred it to *Machaerina* Vahl. Koyama (1956) was the only one of these authors to correctly identify the relationship of this species with the *Lepidosperma* clade. The only other named species in this complex was originally named *Heleocharis* (*Eleocharis*) *halmaturina* J.M.Black by Black (1927) and subsequently transferred to *Tetraria* by Black (1943). *Tetraria monocarpa* (J.M.Black) J.M.Black does not belong to this complex, rather it is a synonym of *Schoenus carsei* Cheeseman (Blake 1943), which is superficially similar to *Tetraria capillaris*.

Netrostylis species have a particularly distinctive persistent style base, similar to those found in *Tetraria s. str.* and this is the main reason that *Netrostylis* was included in *Tetraria* by Black (1934) and this classification was supported by Blake (1943) based on the same character state. Blake (1943) noted the nearly distichous glumes, only one barren flower and minute hypogynous bristles present in some species. However, he particularly emphasised the persistent style base as a character shared with *Tetraria*. The habit is very different from *Tetraria*, more like that of *Neesenbeckia* and some *Machaerina* and *Lepidosperma* species where the leaves are reduced to bracts and the culms are terete or angled. These similarities are sufficiently close that Bentham (1878) included some material of *Netrostylis* in his new species *Lepidosperma leptostachyum* Benth. (Barrett and Wilson 2012).

Netrostylis is sister to the monotypic genus *Neesenbeckia* Levyns, endemic to the Cape Province of South Africa, which has a 6-fid style and the persistent style base on the nutlet is prominently 6-ribbed, smooth and white (Browning and Goetghebeur 2017). *Netrostylis* is allied to *Lepidosperma*, a genus with a very similar distribution that can be distinguished by the six (or three in *L. forsythii* A.A.Ham.) thickened, divided hypogynous scales at the base of the nutlet (Barrett *et al.* 2012c). *Netrostylis* also has affinities with *Machaerina* Vahl (including *Baumea* Gaudich.) which can be distinguished by the new ramets growing out at similar depth to parent ramet, fruit with spongy exocarps, and the lack of a fusiform, persistent style base (Larridon *et al.* 2021b).

Methods

Relevant specimens have been examined by the authors at: AD, AK, B, BM, BRI, CANB, CHR, DBN, FI, G, HO, HBG, K, L, LD, MEL, NE, NSW, P and PERTH. The description is based on herbarium material, however *N. capillaris* and *N. halmaturina* have also been examined in the field by the authors.

Key to genera in the *Lepidosperma* clade

1. Two middle glumes larger than others; perianth of 6 bristles equal to or longer than the nutlet; stigma 6-fid ..... ***Neesenbeckia***

1: Glumes of increasing length from the base, upper glumes the largest; perianth of thickened scales persistent at base of nutlet or bristles 0–5, shorter than the nutlet; stigma (2-)3-fid..... 2

2. Perianth of thickened scales persistent at base of nutlet; style base usually cap-like on nutlet (conical to pyramidal only in *L. evansianum* and *L. rostratum*) ..... ***Lepidosperma***

2: Perianth absent, of flattened scales, or of 1–5 bristles; style base persistent, shortly pyramidal or spindle-like..... 3

3. New ramets growing out at similar depth to parent ramet; style base shortly pyramidal (continuous with nutlet apex) ..... ***Machaerina***

3: New ramets growing out above parent ramet (candelabriform); style base spindle-shaped (constricted at base)..... ***Netrostylis***

Taxonomy

Netrostylis R.L.Barrett, J.J.Bruhl & K.L.Wilson, ***gen. nov.***

Type species: *Netrostylis capillaris* (F.Muell.) R.L.Barrett, J.J.Bruhl & K.L.Wilson (based on *Chaetospora capillaris* F.Muell.).

Tufted stoloniferous perennials, usually less than 1 m high (rarely to 1.6 m), rhizome tightly clumping to spreading, new culms within a ramet arising slightly higher than the parent culm resulting in a compact candelabrum arrangement. New ramets forming from long rhizomes. *Culms* scapose. Culms and leaves erect to spreading, terete or quadrangular, capilliform and decumbent to rigid and erect. *Leaves* basal; blade usually strongly reduced on the sheath (rarely to 3 cm long), ligule present, cleft. *Inflorescence* open or contracted paniculate, usually pseudolateral (sometimes appearing to be terminal and spicately condensed), usually with few spikelets. Primary bracts usually short, occasionally long, sheathing, often sub-erect. *Spikelets* with several spirally arranged, long persistent glumes of increasing length, upper 1 or 2 glumes each subtending a flower, enclosed by the wings of the next glume. Lower flower functionally male, upper (occasionally 2) flower(s) bisexual. Bristles absent or filiform. Hypogynous scales present, united and thickened only at the base, forming a small ring or cup fused to the base of the nutlet, sometimes producing 3 flat scales or up to 5 filiform, barbellulate bristles; *Stamens* 3. *Style* (2-)3-fid, hairy; style base distinct, much thickened, persistent, papillose-tuberculate. *Nutlet* ovate, rounded 3-angular, surface usually smooth below, usually scabrous on persistent, spindle-shaped style base. (Figures 1, 2)

Diagnostic characters: Related to *Neesenbeckia* Levyns, differing in the style being (2-)3-fid (*vs* 6-fid); the style base being spindle-shaped (*vs* variously swollen and 6 ribbed), usually papillose (*vs* glabrous), and brown (*vs* white); 3 stamens (*vs* 6); and candelabriform, slender (*vs* lateral, robust) rhizomes.

Distribution: A genus of about eleven species in Australia and New Zealand, most still undescribed (Barrett *et al*. 2012b). A revision currently in preparation plans to recognise five species endemic to south-western Australia, three species endemic to south-eastern Australia, two species endemic to north-eastern Australia and one endemic to New Zealand.

Etymology: Derived from the Greek *netron* (spindle) and *stylis* (style) in reference to the spindle-shaped style base persistent on the nutlets of this genus. Thus derived, *Netrostylis* is feminine (see Turland *et al*. 2018; Art. 62.2) as is *Tetraria*, so no alterations of epithet terminations are required for the two species transferred from that genus.

Fig. 1. A. *Netrostylis capillaris* spikelet (sp) with emergent style branches (sbr) and mature nutlet (nl) with ring-like persistent perianth (pr) and stout, elongated style base (sb). B. *Netrostylis halmaturina* fertile glumes (gl); immature style base (persistent base on nutlet with apex broken off) (sb); stamen (st); perianth filament (pf); and immature nutlet (nl). Vouchers: A: Rosebery, Tasmania, *S.T. Blake 18431* (BRI AQ156882); B: Cherry Gardens, South Australia, *J.B. Cleland s.n.* (BRI AQ156881). Photos by R.L. Barrett.

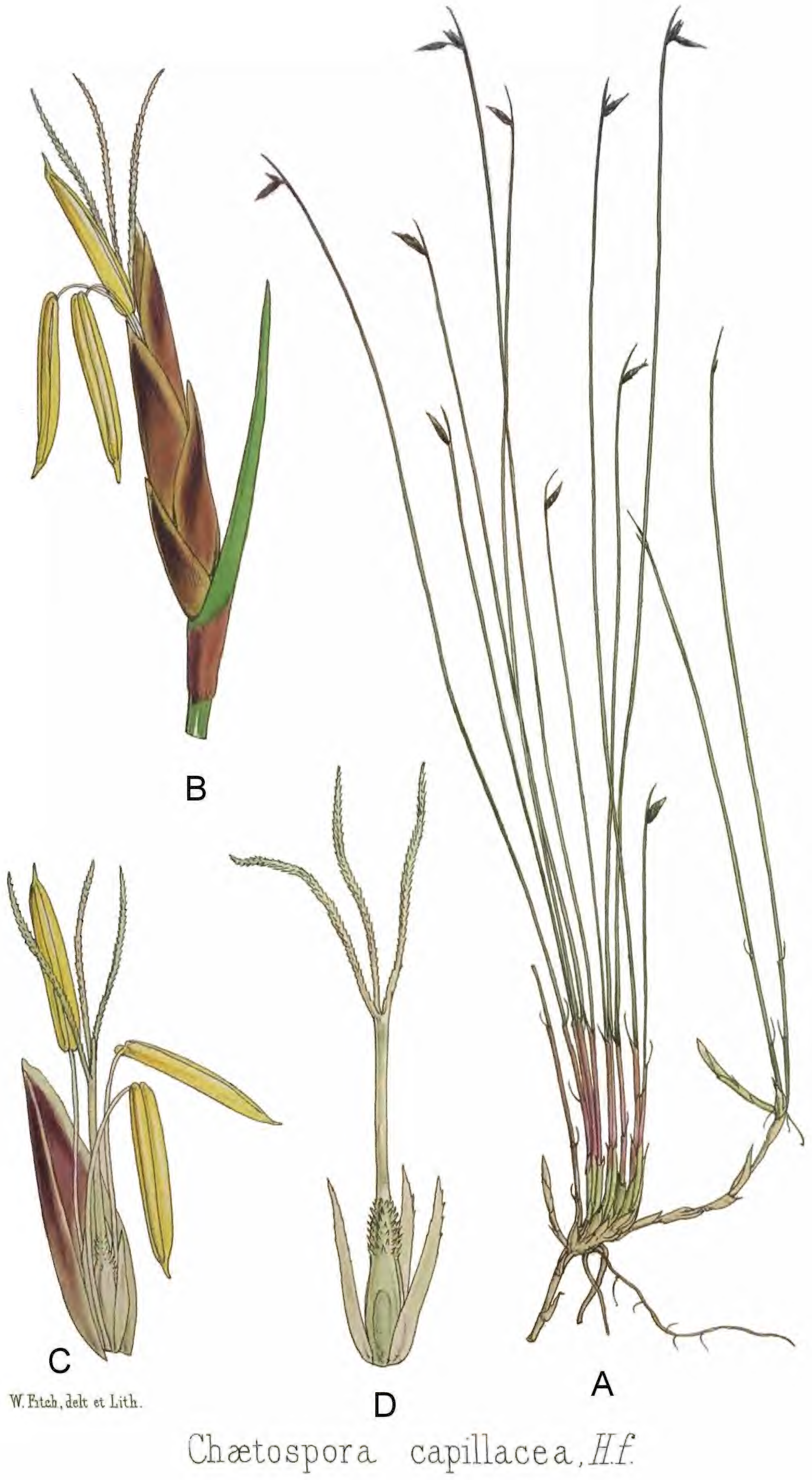

Fig. 2. *Netrostylis capillaris*. A. Habit. B. Fertile spikelet. C. Fertile glume and flower. D. Style, ovary and perianth scales. Reproduced and re-arranged from Hooker (1858: Tab. CXLI).

Affinities: Most closely allied to the monotypic genus *Neesenbeckia* Levyns. *Netrostylis* is distinguished from *Neesenbeckia* by the spindle-shaped persistent style base on the nutlet. *Neesenbeckia* has a distinctive (large when young), smooth, white, persistent style base on the nutlet, which is prominently 6-ribbed, and the style is also 6-fid (Browning and Goetghebeur 2017) versus (2-)3-fid in *Netrostylis*). The slender rhizome is characterised by an unusual candelabrum-type development. Each new shoot arises beside the parent shoot, but usually a little higher than the parent, creating a candelabrum shape. These candelabriform rhizomes of *Netrostylis* are quite distinctive and make it possible to recognise the genus from sterile specimens.

Netrostylis is otherwise allied to *Lepidosperma* which is easily distinguished by the hypogynous scales, which are thickened at the base but not or scarcely fused around the base of the nutlet. In some *Netrostylis* species, a prominent ring or cup-shaped base fused to the nutlet (often breaking off at maturity) is probably analogous to the hypogynous scales found in *Lepidosperma*, but this structure only sometimes produces 3 broad, thin scales or up to 5 filiform bristles. *Lepidosperma rostratum* S.T.Blake is unusual in having a rostrate persistent style base covered in fine papillae somewhat similar to that of *Netrostylis* (though lacking the fusiform apex), but genetic data place this taxon within *Lepidosperma* (Barrett *et al*., 2012c).

Netrostylis also has affinities with *Machaerina* Vahl (including *Baumea* Gaudich.). *Machaerina* can be distinguished by the fruit with spongy exocarp and the lack of a fusiform, persistent style base. *Baumea* has consistently been resolved within *Machaerina* in phylogenetic studies (e.g. Viljoen *et al*. 2013; Larridon *et al*. 2021b).

Netrostylis capillaris s.l. is similar in appearance to *Schoenus carsei,* which has a similar distribution in New Zealand, but a more restricted distribution in southern Australia relative to *Netrostylis*. When fertile, the two are readily distinguished by the flexuous rachilla and absence of a persistent style base on the nutlet in *S. carsei*, but the differences are more subtle in sterile specimens. When fresh, the culms of *Schoenus carsei* are 'striped' longitudinally with whitish stomatal zones alternating with yellow-green non-stomatal zones, but this is less obvious when dried. The culms of *Netrostylis* are relatively uniform in colour, stomatal zones rarely being strongly evident. A leaf ligule is present in *S. carsei* and in *N. capillaris*, but in the latter has a free limb that is cleft more or less in the middle. The persistent sheaths on the rhizome are usually straw-coloured in *N. capillaris* and light to dark brown in *S. carsei*. Gardner (1998a, 1998b) provides four additional useful vegetative characters to recognise *N. capillaris* (*vs S. carsei*) in New Zealand: culms usually <0.8 (*vs* 0.8–2) mm diam.; pith of culms finely but distinctly septate (*vs* continuous); reduced leaf blade <5 (*vs* 10–30) mm long; and the margins at the apex of the leaf sheath minutely setose (*vs* glabrous). In New Zealand, these species may grow together, but in Australia, *S. carsei* tends to grow in wetter habitats than *Netrostylis capillaris*.

Netrostylis capillaris (F.Muell.) R.L.Barrett, J.J.Bruhl & K.L.Wilson, ***comb. nov***.

Basionym: *Chaetospora capillaris* F.Muell., *Fragm.* 9: 34 (1875), based on *Chaetospora capillacea* Hook.f., *Fl. Tasman.* 2(2): 81 ([1858] 1859), *nom. illeg. non* Nees (1834); *Elynanthus capillaceus* Benth., *Fl. Austral.* 7: 377 (1878); *Schoenus capillaris* (F.Muell.) F.Muell., *Syst. Census Austral. Pl.* 128 (1882), *nom. illeg., non* Sw. (1788); *Cladium capillaceum* C.B.Clarke ex Cheeseman, *Man. New Zealand Fl.* 789 (1906); *Mariscus capillaceus* (Hook.f.) Fernald, *Rhodora* 25: 52 (1923); *Machaerina capillacea* T.Koyama, *Bot. Mag. Tokyo* 69: 63 (1956), *nom. illeg., nom. superfl.*; *Tetraria capillaris* (F.Muell.) J.M.Black, *Trans. Royal Soc. S. Austral.* 58: 169 (1934).

Type: Australia: Tasmania: Dry sandy banks by the Kermandie [River], Hospital Bay, south Huon River, [1850s], *A.F. Oldfield 145* (holo: K 000960101!).

Notes: The earliest published epithet for this species, *Chaetospora capillacea* Hook.f. was illegitimate at the time of publication, being a later homonym of *Chaetospora capillacea* Nees (1834), and therefore cannot be transferred to *Netrostylis*, thus the combination is based on Mueller's (1875) replacement epithet.

We have only located a single specimen matching the protologue, so we consider the cited specimen to be a holotype. It bears pencil drawings of the spikelets typical of those made by Hooker, and matching those published with the original description (Figure 2).

Netrostylis halmaturina (J.M.Black) R.L.Barrett, J.J.Bruhl & K.L.Wilson, ***comb. nov.***

Basionym: *Eleocharis halmaturina* J.M.Black, *Trans. Royal Soc. S. Austral.* 51: 378 (1927) (as *Heleocharis*); *Tetraria halmaturina* (J.M.Black) J.M.Black, *Fl. S. Austral.* (edn 2); 1: 153 (1943).

Type: South Australia: Kangaroo Island: Rocky River, 18 November 1924, *J.B. Cleland s.n.* (holo: AD 98018480!; iso: K 000960102!).

Notes: There is only a single collection at AD matching the protologue, and it is unlikely that the duplicate at K had been distributed at the time the species was described, so we consider these sheets to be a holotype and isotype respectively.

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References

Barrett RL, Barrett MD, Wallace MJ, Bruhl JJ, Wilson KL (2012c) A preliminary phylogeny of *Lepidosperma* (Cyperaceae: Schoeneae). Chapter 7 in Barrett RL, (2012). *Systematic studies in Cyperaceae tribe Schoeneae:* Lepidosperma *and allied genera*. PhD Thesis. (School of Plant Biology, The University of Western Australia: Crawley)

Barrett RL, Bruhl JJ, Wilson KL (2012a) Resolution of the phylogenetic position and diversity of the *Tetraria capillaris* complex (Cyperaceae, Schoeneae): molecular evidence for a new genus and ten new species. Chapter 8 in Barrett RL, (2012). *Systematic studies in Cyperaceae tribe Schoeneae:* Lepidosperma *and allied genera*. PhD Thesis. (School of Plant Biology, The University of Western Australia: Crawley)

Barrett RL, Bruhl JJ, Wilson KL (2012b) Taxonomic revision of *Netrostylis*, a new Australasian genus of Cyperaceae tribe Schoeneae. Chapter 9 in Barrett RL, (2012). *Systematic studies in Cyperaceae tribe Schoeneae:* Lepidosperma *and allied genera*. PhD Thesis. (School of Plant Biology, The University of Western Australia: Crawley)

Barrett RL, Bruhl JJ, Wilson KL (2021) Revised generic delimitation of Schoeneae subtribe Tricostulariinae (Cyperaceae) with description of a new Australian genus *Ammothryon* and new species of *Tricostularia*. *Telopea* 24: https://doi.org/10.7751/telopea14454 In press.

Barrett RL, Wilson KL (2012) A review of the genus *Lepidosperma* (Schoeneae: Cyperaceae). *Australian Systematic Botany* 25: 225–294. https://doi.org/10.1071/SB11037

Barrett RL, Wilson KL, Bruhl JJ (2019) *Anthelepis*, a new genus for four mainly tropical species of Cyperaceae from Australia, New Caledonia and South East Asia. *Australian Systematic Botany* 32: 269–289. https://doi.org/10.1071/SB18047

Bentham G (1878) *Flora Australiensis: A description of the plants of the Australian Territory. Vol. VII. Roxburghiaceae to Filices*. (Lovell Reeve: London) https://doi.org/10.5962/bhl.title.141

Black JM (1927) Additions to the flora of South Australia No. 25. *Transactions of the Royal Society of South Australia* 51: 378–385. https://www.biodiversitylibrary.org/item/129843#page/400/mode/1up

Black JM (1934) Additions to the flora of South Australia No. 32. *Transactions of the Royal Society of South Australia* 58: 168–186. https://www.biodiversitylibrary.org/item/129835#page/192/mode/1up

Black JM (1943) *Flora of South Australia Part 1.* (edn 2). (Government Printer: Adelaide)

Blake ST (1943) Critical notes on the Gramineae and Cyperaceae of South Australia with descriptions of new species. *Transactions of the Royal Society of South Australia* 67: 42–61. https://www.biodiversitylibrary.org/item/129832#page/54/mode/1up

Browning J, Goetghebeur G (2017) *Sedge (Cyperaceae) genera of Africa and Madagascar*. (Troubador Publishing: Leicester, UK)

Bruhl JJ (1995) Sedge genera of the world: relationships and a new classification of the Cyperaceae. Australian Systematic Botany 8: 125–305. https://doi.org/10.1071/SB9950125

Cheeseman TF (1906) *Manual of the New Zealand Flora*. (John Mackay, Government Printer: Wellington) https://www.biodiversitylibrary.org/item/44765#page/5/mode/1up

Elliott TL, Barrett RL, Muasya AM (2019) A taxonomic revision of *Schoenus cuspidatus* and allies (Cyperaceae, tribe Schoeneae) –– Part 1. *South African Journal of Botany* 121: 519–535. https://doi.org/10.1016/j.sajb.2018.11.021

Elliott TL, Muasya AM (2017) Taxonomic realignment in the southern African *Tetraria* (Cyperaceae, tribe Schoeneae; *Schoenus* clade). *South African Journal of Botany* 112: 354–360. http://dx.doi.org/10.1016/j.sajb.2017.06.011

Elliott TL, Muasya AM (2018) A taxonomic revision of *Schoenus compar* - *Schoenus pictus* and allies (Cyperaceae, tribe Schoeneae) with three new species described from South Africa. *South African Journal of Botany* 114: 303–315. https://doi.org/10.1016/j.sajb.2017.11.020

Elliott TL, Muasya AM (2019) Three new species and a new combination among Southern African *Schoenus* (Cyperaceae, tribe Schoeneae). *Phytotaxa* 401: 267–275. https://doi.org/10.11646/phytotaxa.401.4.4

Elliott TL, Muasya AM (2020) A taxonomic revision of the *Epischoenus* group of *Schoenus* (Cyperaceae, tribe Schoeneae). *South African Journal of Botany* 135: 296–316. https://doi.org/10.1016/j.sajb.2020.08.029

Elliott TL, van Mazijk R, Barrett RL, Bruhl JJ, Joly S, Muthaphuli N, Wilson KL, Muasya AM (2021) Global dispersal and diversification of the genus *Schoenus* (Cyperaceae) from the Western Australian biodiversity hotspot. *Journal of Systematics and Evolution* Online early. https://doi.org10.1111/jse.12742.

Gardner RO (1998a) *Schoenus carsei* and *Tetraria capillaris*. *Auckland Botanical Society Journal* 53: 38–40.

Gardner RO (1998b) *Schoenus carsei* revisited. *Auckland Botanical Society Journal* 53: 56–57.

Goetghebeur P (1998) Cyperaceae. Pp. 141–190 in K Kubitzki, H Huber, PJ Rudall, PS Stevens and T Stützel (Eds) *The families and genera of Vascular plants*. (Springer-Verlag: Berlin)

Hooker JD (1858) *The botany of the Antarctic voyage of H.M. Discovery Ships 'Erebus' and 'Terror', in the years 1839–1843, under the command of Captain Sir James Clark Ross. Part III. Flora Tasmaniae. Vol. II. monocotyledons and acotyledons*. (Reeve: London) https://www.biodiversitylibrary.org/item/90344#page/1/mode/1up

Koyama TM (1956) Taxonomic studies of the Cyperaceae V. § 12. A new classification of the genus *Cladium* in a wide meaning. *The Botanical Magazine, Tokyo* 69: 59–67.

Larridon I, Bauters K, Semmouri I, Viljoen J-A, Prychid CJ, Muasya AM, Bruhl JJ, Wilson KL, Senterrehi B, Goetghebeur PA (2018a) Molecular phylogenetics of the genus *Costularia* (Schoeneae, Cyperaceae) reveals multiple distinct evolutionary lineages. *Molecular Phylogenetics and Evolution* 126: 196–209. https://doi.org/10.1016/j.ympev.2018.04.016

Larridon I, Rabarivola L, Xanthos M, Muasya AM (2019) Revision of the Afro-Madagascan genus *Costularia* (Schoeneae, Cyperaceae): infrageneric relationships and species delimitation. *PeerJ* 7: e6528. https://doi.org/10.7717/peerj.6528

Larridon I, Verboom GA, Muasya AM (2017) (2555) Proposal to conserve the name *Tetraria* (Cyperaceae) with a conserved type. *Taxon* 66: 1226–1227. https://doi.org/10.12705/665.22

Larridon I, Verboom GA, Muasya AM (2018b) Revised delimitation of the genus *Tetraria*, nom. cons. prop. (Cyperaceae, tribe Schoeneae, *Tricostularia* clade). *South African Journal of Botany* 118: 18–22. https://doi.org/10.1016/j.sajb.2018.06.007

Larridon I, Zuntini AR, Barrett RL, Wilson KL, Bruhl JJ, Goetghebeur P, Baker WJ, Brewer GE, Epitawalage N, Fairlie I, Forest F, Kikuchi I, Pokorny L, Spalink D, Simpson DA, Muasya AM, Roalson EH (2021a) Resolving the generic limits in Cyperaceae tribe Abildgaardieae using targeted sequencing. *Botanical Journal of the Linnean Society* Online Early. https://doi.org/10.1093/botlinnean/boaa099

Larridon I, Zuntini AR, Léveillé-Bourret E, Barrett RL, Starr JR, Muasya AM, Villaverde T, Bauters K, Brewer GE, Bruhl JJ, Costa SM, Elliott TL, Epitawalage N, Escudero M, Fairlie I, Goetghebeur P, Hipp AL, Jiménez-Mejías P, Sabino Kikuchi IAB, Luceño M, Márquez-Corro JI, Martín-Bravo S, Maurin O, Pokorny L, Roalson EH, Semmouri I, Simpson DA, Spalink D, Thomas WW, Wilson KL, Xanthos M, Forest F, Baker WJ (2021b) A new classification of Cyperaceae (Poales) supported by phylogenomic data. *Journal of Systematics and Evolution*: JSE-2020-09-229. In press.

Levyns MR (1947) *Tetraria* and related genera, with special reference to the flora of the Cape Peninsula. *Journal of South African Botany* **13:** 73–93.

Moore LB, Edgar E (1970) *Flora of New Zealand. Vol. II*. (Government Printer: Wellington)

Muasya AM (2016) The changing generic concepts in Cyperaceae — Cosmopolitan mega-genera and polyphyly of southern African taxa. *South African Journal of Botany* 103: 337. https://doi.org/10.1016/j.sajb.2016.02.125

Muasya AM, Simpson DA, Verboom GA, Goetghebeur P, Naczi RFC, Chase MW, Smets EF (2009) Phylogeny of Cyperaceae based on DNA sequence data: current progress and future prospects. *The Botanical Review* 75: 2–21. https://doi.org/10.1007/s12229-008-9019-3

Mueller FJH von (1875) *Fragmenta Phytographiae Australiae. Vol. 9*. (Melbourne Printers: Melbourne) https://www.biodiversitylibrary.org/item/7226#page/1/mode/1up

Nees von Esenbeck CGD (1834) Übersicht der Cyperaceengattungen. *Linnaea* 9: 273–306. https://www.biodiversitylibrary.org/item/109555#page/279/mode/1up

Rye BL (1987) Cyperaceae. Pp. 870–906 in NG Marchant and JR Wheeler (Eds) *Flora of the Perth Region*. (Western Australian Herbarium: Perth)

Semmouri I, Bauters K, Léveillé-Bourret É, Starr JR, Goetghebeur P, Larridon I (2019) Phylogeny and systematics of Cyperaceae, the evolution and importance of embryo morphology. *Botanical Review* 85: 1–39. https://doi.org/10.1007/s12229-018-9202-0

Slingsby JA, Verboom GA (2006) Phylogenetic relatedness limits co-occurrence at fine spatial scales: evidence from the schoenoid sedges (Cyperaceae: Schoeneae) of the Cape Floristic Region, South Africa. *The American Naturalist* 168: 14–27. https://doi.org/10.1086/505158

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AK, Prado J, Price MJ, Smith GF (2018) (Eds) *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159*. (Koeltz Botanical Books: Glashütten) https://doi.org/10.12705/Code.2018

Verboom GA (2006) A phylogeny of the schoenoid sedges (Cyperaceae: Schoeneae) based on plastid DNA sequences, with special reference to the genera found in Africa. *Molecular Phylogenetics and Evolution* 38: 79–89. https://doi.org/10.1016/j.ympev.2005.05.012

Viljoen J-A, Muasya AM, Barrett RL, Bruhl JJ, Gibbs AK, Slingsby JA, Wilson KL, Verboom AG (2013) Radiation and repeated transoceanic dispersal of Schoeneae (Cyperaceae) through the Southern Hemisphere. *American Journal of Botany* 100: 2494–2508. https://doi.org/10.3732/ajb.1300105

Wheeler JR, Graham L (2002) Cyperaceae. Pp. 263–298 in JR Wheeler (Ed.) *Flora of the South West. Bunbury, Augusta, Denmark. Flora of Australia Supplementary Series 12*. (Australian Biological Resources Study, Canberra, Conservation and Land Management, Como and University of Western Australia Press: Crawley)

Wilson KL (1993) Cyperaceae. Pp. 293–396 in GJ Harden (Ed.) *Flora of New South Wales*. (University of New South Wales Press: Kensington)

Wilson KL (1994) Cyperaceae. Pp. 238–356 in NG Walsh and TJ Entwisle (Ed.) *Flora of Victoria Volume 2. Ferns and allied plants, conifers and monocotyledons*. (Inkata Press: Melbourne)

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Revision of generic concepts in Schoeneae subtribe Tricostulariinae (Cyperaceae) with a new Australian genus *Ammothryon* and new species of *Tricostularia*

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Abstract

The *Tricostularia* Nees ex Lehm. group of genera is reviewed and formally recognised as Cyperaceae tribe Schoeneae subtribe Tricostulariinae R.L.Barrett, K.L.Wilson & J.J.Bruhl. Molecular data from plastid *rbc*L and *trnL–F* and nuclear ITS and ETS regions are combined with a novel assessment of morphological characters to support our new classification. Six genera are included: a new genus, *Ammothryon* R.L.Barrett, K.L.Wilson & J.J.Bruhl, and the named genera *Chaetospora* R.Br., *Morelotia* Gaudich., *Tetraria* P.Beauv., *Tricostularia*, and *Xyroschoenus* Larridon. *Ammothryon*, *Chaetospora* and *Tricostularia* are all endemic to southern Australia. *Morelotia* has one species each in Hawaii, French Polynesia and New Zealand, and three species in south-west Western Australia. *Tetraria* has a disjunct distribution in Southern Africa, Borneo, New Guinea and New Caledonia. *Xyroschoenus* is endemic to the Seychelles. *Tetrariopsis* C.B.Clarke (based on *Tetrariopsis octandra* (Nees) C.B.Clarke) is included under an expanded concept of *Morelotia*, which also includes *Tetraria australiensis* C.B.Clarke and *Tetraria microcarpa* S.T.Blake from south-west Western Australia. *Tricostularia bennettiana* R.L.Barrett & K.L.Wilson, *Tricostularia davisii* R.L.Barrett & K.L.Wilson, *Tricostularia lepschii* R.L.Barrett & K.L.Wilson, *Tricostularia newbeyi* R.L.Barrett & K.L.Wilson, and *Tricostularia sandifordiana* R.L.Barrett & K.L.Wilson are described as new species from south-west Western Australia. The following new combinations are made: *Ammothryon grandiflorum* (Nees ex Lehm.) R.L.Barrett, K.L.Wilson & J.J.Bruhl, *Morelotia australiensis* (C.B.Clarke) R.L.Barrett & K.L.Wilson, *Morelotia microcarpa* (S.T.Blake) R.L.Barrett & K.L.Wilson, *Morelotia octandra* (Nees) R.L.Barrett & J.J.Bruhl and *Tricostularia drummondii* (Steud.) R.L.Barrett & K.L.Wilson. *Tricostularia drummondii* is reinstated from synonymy (formerly *Discopodium drummondii* Steud.), having previously been confused with *T. exsul* (C.B.Clarke) K.L.Wilson & R.L.Barrett. Lectotypes are selected for *Chaetospora flexuosa* var. *gracilis* Boeckeler, *Discopodium drummondii* Steud., *Elynanthus grandiflorus* Nees ex Lehm., *Lampocarya affinis* Brongn., *Lepidosperma exsul* C.B.Clarke, *Morelotia gahniiformis* Gaudich. var. *minor* A.Rich., *Tetraria australiensis* C.B.Clarke, *Tetraria capillacea* var. *intercedens* Kük., *Tricostularia compressa* Nees ex Lehm. and *Tricostularia neesii* Lehm.

Keywords: *Chaetospora*; *Costularia*; *Gahnia*; *Lophoschoenus*; *Machaerina*; *Morelotia*; *Schoenus*; *Tetraria*; *Tetrariopsis*; *Xyroschoenus*; Plant systematics; Taxonomy; Morphology; Sedge; Australia; Borneo; French Polynesia; Hawaii; New Caledonia; New Guinea; New Zealand; Seychelles; Southern Africa.

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Introduction

Cyperaceae tribe Schoeneae has been characterised by very high levels of morphological variability, combined with high species diversity (over 600 species; Govaerts *et al.* 2020; R.L. Barrett *et al.* unpubl. data). Circumscription of many genera has remained problematic in morphological classifications, and the relationships between genera have been very uncertain (Bruhl 1995; Goetghebeur 1986, 1998). The widespread uptake of molecular sequencing methods has provided many new, and sometimes unexpected, insights into relationships within Schoeneae (Zhang *et al.* 2004, 2007; Slingsby and Verboom 2006; Verboom 2006; Bruhl *et al.* 2008a, 2008b; Simpson *et al.* 2008; Barrett 2012; Viljoen *et al.* 2013; Muasya 2016; Musili *et al.* 2016; Barrett *et al.* 2017, 2019, 2020, 2021a, 2021b; Semmouri *et al.* 2019). Many genera have been revealed to be paraphyletic, requiring considerable re-circumscription across the tribe (Wilson *et al.* 2012; Elliott and Muasya 2017, 2018, 2019; Larridon *et. al.* 2018a, 2018b, 2019; Elliott *et al.* 2019; Barrett *et al.* 2019, 2020). Increased sampling in phylogenies, and targeted sequencing of 100s of loci is now providing resolution for many previously poorly resolved relationships within Cyperaceae (Larridon *et al.* 2020, 2021a, 2021b; Villaverde *et al.* 2020; Costa *et al.* 2021).

The conclusions reached here are the combination of considerable time studying herbarium material around the world, extensive literature searches, and extensive fieldwork, supported by molecular phylogenetic data. Many Schoeneae genera, as traditionally circumscribed, have species that are now placed in quite distantly related groups within the tribe, so reference to past synonyms can be an ongoing source of confusion for understanding relationships. We here propose that recognition of subtribes will assist in defining the most significant relationships within Schoeneae, and provide a basis for careful re-examination of morphological diversity and homology across the tribe. Most subtribe names will be validated in a forthcoming paper providing a new global classification of Cyperaceae, to which this paper is a precursor (Larridon *et al.* 2021b). Here we define the new subtribe Tricostulariinae R.L.Barrett, K.L.Wilson & J.J.Bruhl with six constituent genera (Table 1): the new genus *Ammothryon* R.L.Barrett, K.L.Wilson & J.J.Bruhl, and the named genera *Chaetospora* R.Br., *Morelotia* Gaudich., *Tetraria* P.Beauv., *Tricostularia* Nees ex Lehm., and *Xyroschoenus* Larridon. The delimitation of each of the genera accepted here has only recently been refined (Larridon *et al.* 2018a, 2018b; Barrett *et al.* 2020) or is newly defined in this paper. The *Tricostularia* clade has a crown node age of around 28.4 (19.8–39.2) Ma (Larridon *et al.* 2018a). Viljoen *et al.* (2013) found that this clade most likely originated in Australia, with the current distribution of genera outside Australia most likely due to long-distance dispersal events. Estimates should be revised now that more molecular data are available and fossils such as *Gahniocarpus* Benl (Benl 1942) should be evaluated to determine whether they can be used to time-calibrate the phylogeny of tribe Schoeneae as there is still a general lack of good fossils for many clades of Cyperaceae (Smith *et al.* 2010).

Table 1. Genera in subtribe Tricostulariinae with number of species, number of sequenced species represented in this paper, estimated crown / node divergence age in millions of years (Ma; from Larridon *et al.* 2018a) and general distribution.

Genus	No. of species	No. sequenced	Divergence age	Distribution
Tricostulariinae	*c.* 66	50 (76%)	58 / 28 Ma	Africa, Asia, Australia, Pacific
Ammothryon	1	1 (100%)	22 / – Ma	South-west Australia
Chaetospora	3	2 (67%)	25 / – Ma	Southern Australia
Morelotia	6	4 (67%)	17 / 5 Ma	South-west Australia, New Zealand, Rapa Iti, Hawaii
Tetraria	*c.* 39	32(+) (82%)	20 / 17 Ma	New Caledonia, Malesia, Southern Africa
Tricostularia	*c.* 16	10 (62%)	25 / – Ma	Southern Australia
Xyroschoenus	1	1 (100%)	17 / – Ma	Seychelles

Within the *Tricostularia* clade, the most significant taxonomic changes over time have been in the genus *Tetraria*, which has been difficult to define prior to detailed phylogenetic studies. *Tetraria* has been considered a primarily southern African genus, though numerous segregates have been recognised even within that region: *Schoenopsis* P.Beauv. ex T.Lestib. (Lestiboudois 1819); *Lepisia* C.Presl (Presl 1829); *Sclerochaetium* Nees (1832); *Aulacorhynchus* Nees (Nees 1834) and *Boeckeleria* T.Durand (Durand 1888). The genus *Lophoschoenus* Stapf was proposed for species from New Caledonia originally described under *Schoenus* L. (Stapf and Turrill 1914). Kükenthal (1939a) reduced *Lophoschoenus* to a subgenus of *Costularia* C.B.Clarke, a position followed by Raynal (1974) when he described several additional species. Taxa in the *Lophoschoenus* clade have recently been incorporated into a modified definition of *Tetraria* (Larridon *et al.* 2018b).

Several miscellaneous species from Australian and Borneo have also been included under *Tetraria*: *T. australiensis* C.B.Clarke (Clarke 1908); *T. octandra* (Nees) Kük. (Kükenthal 1931); *Tetraria capillaris* (F.Muell.) J.M.Black and *T. monocarpa* (J.M.Black) J.M.Black (Black 1934); *T. halmaturina* (J.M.Black) J.M.Black (Black

1943); *T. microcarpa* S.T.Blake (Blake 1949) and *T. borneensis* Kern (Kern 1958). Clarke (1908) established the genus *Tetrariopsis* C.B.Clarke for *Tetraria octandra*, a classification that has been supported by some authors (e.g. Bruhl 1995; Barrett and Pin Tay 2016; Larridon *et al.* 2018a). The morphological distinctions between *Morelotia* and *Tetrariopsis* given by Larridon *et al.* (2018a) break down with the examination of more species. A new classification has just been published for *T. capillaris* and *T. halmaturina*, placing them in a new genus, *Netrostylis* R.L.Barrett, J.J.Bruhl & K.L.Wilson (R.L.Barrett *et al.* 2021a). *Tetraria monocarpa* is generally considered to be a synonym of *Schoenus carsei* Cheeseman (R.L.Barrett *et al.* 2021a). The exact position of *T. borneensis* J.Kern is a matter of ongoing study by R.L. Barrett and I. Larridon after its phylogenetic position was resolved within the *Caustis* clade by Larridon *et al.* (2018a).

While a relatively stable classification of *Tetraria* has been in use in southern Africa for many decades (Levyns 1947; Podlech 1967; Bond and Goldblatt 1984; Forbes 1987; Gordon-Gray 1995; Archer 2000, 2003; Govaerts *et al.* 2007), molecular data revealed that a large clade of these species, including the type species, actually belong to the *Schoenus* L. clade (Slingsby and Verboom 2006; Verboom 2006; Muasya *et al.* 2000, 2009; Viljoen *et al.* 2013; Slingsby *et al.* 2014; Larridon *et al.* 2018a; Semmouri *et al.* 2019). Most species of *Epischoenus* C.B.Clarke (see Levyns 1959) also belong in *Schoenus*, as suggested by Browning and Gordon-Gray (1995) on morphological grounds, but *E. cernuus* Levyns has been shown to belong in *Tetraria* (Verboom 2006; Muasya *et al.* 2009; Viljoen *et al.* 2013; Larridon *et al.* 2018a). The species found to belong in *Schoenus* were transferred there by Elliott and Muasya (2017, 2019) and revised by Elliott and Muasya (2020). As this included the accepted type species of *Tetraria*, to avoid the loss of this iconic genus name from the South African flora, Larridon *et al.* (2017a) have proposed *T. thermalis* (L.) C.B.Clarke as a conserved type, a position followed here pending a formal decision on the proposal by the nomenclature committees.

The concept of the genus *Tricostularia* is here restricted to species occurring in southern Australia, all but one of the species being endemic to the south-west of Western Australia. Following study of the type specimens and analysis of DNA sequence data, *Lepidosperma aphylla* R.Br. and *L. exsul* C.B.Clarke were transferred to *Tricostularia* (Barrett and Wilson 2012). *Tricostularia guillauminii* (Kük.) J.Raynal, *T. paludosa* (R.Br.) Benth. and the widespread *T. undulata* (Thwaites) J.Kern (see Liang *et al.* 2010) have recently been transferred to the new genus *Anthelepis* R.L.Barrett, K.L.Wilson & J.J.Bruhl (Barrett *et al.* 2019). Five named species are currently recognised in *Tricostularia* and five additional phrase-named taxa have been recognised in Western Australia since 2013. Evidence is presented for an expanded number of taxa in the genus, with the recognition of at least four currently unnamed species supported. Detailed morphological examination of specimens suggests around 16 species should be recognised (R.L. Barrett unpubl. data). A full taxonomic revision of the genus is recommended, but further fieldwork is required to assess the taxonomy of a number of anomalous specimens.

Materials and methods

Morphology

Morphological descriptions have been prepared primarily on the basis of material held at NSW, with additional examination of specimens at AD, B, BM, BRI, CANB, CGE, G, HBG, K, L, LD, MEL, NE, NSW, NY, P and PERTH. Images of all specimens available through herbarium online databases listed in Table 2 have been examined and are indicated by * in specimen citations. All specimens cited have been seen unless otherwise indicated as *n.v.* Most of the species treated here have also been examined in the field by at least one of the authors.

Table 2. Online databases where specimen images have been examined for this study.

Database	Website	Date accessed
Auckland War Memorial Museum (AK)	https://www.aucklandmuseum.com/discover/collections-online/search	Sept. 2020
Australasian Virtual Herbarium	https://avh.ala.org.au/	May 2020
Herbarium Berolinense, Berlin Botanic Garden (B)	http://ww2.bgbm.org/Herbarium/default.cfm	May 2020
The Natural History Museum (BM)	https://data.nhm.ac.uk/dataset/collection-specimens	May 2020
Consortium of Pacific Herbaria	https://serv.biokic.asu.edu/pacific/portal/collections/index.php	May 2020
University Halle (HAL)	https://www.botanik.uni-halle.de/herbarium/93690_2831895/	May 2020
JSTOR Global Plants	https://plants.jstor.org	June 2020
Royal Botanic Gardens, Kew (K)	http://apps.kew.org/herbcat/gotoHomePage.do	May 2020
Naturalis (L, U)	http://bioportal.naturalis.nl	June 2020

Database	Website	Date accessed
New York Botanic Garden (NY)	http://sweetgum.nybg.org/science/vh/	May 2020
Muséum National d'Histoire Naturelle (P)	https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form?lang=en_US	June 2020
National Tropical Botanic Garden (NTBG)	https://ntbg.org/database/herbarium/	June 2020
Herbier de la Polynésie française (PAP)	http://nadeaud.ilm.pf/	June 2020
Sweden's Virtual Herbarium	http://herbarium.emg.umu.se/standard_search.html	May 2020
National Museum of Natural History, Smithsonian Institute (US)	https://collections.nmnh.si.edu/search/botany/#new-search	May 2020
Museum of New Zealand, Te Papa Tongarewa (WELT)	https://collections.tepapa.govt.nz/search/	Sept. 2020
Zürich Herbaria (Z, ZSS, ZT)	https://www.herbarien.uzh.ch/en/belegsuche.html	Oct. 2020

DNA extraction

All taxa newly sampled for this study and sequences obtained from GenBank are represented by voucher specimens as detailed in Table 3.

Table 3. Taxa analysed, sequence region, vouchers and GenBank reference numbers. Most vouchers also have duplicates at other herbaria.

Name	Voucher	*rbcL*	*trnL-F*	ITS	ETS
Ammothryon grandiflorum (Nees ex Lehm.) R.L.Barrett, K.L.Wilson & J.J.Bruhl	Western Australia, *Barrett* RLB 3364 (PERTH)	–	KF553525, MW589143	KF553459	KF553576, MW588442
Ammothryon grandiflorum	Western Australia, *Wilson* 8847 (NSW)	–	KF553525	–	–
Chaetospora curvifolia R.Br.	Western Australia, *Barrett* RLB 4174 (PERTH)	–	MW589144	KF553457	–
Chaetospora curvifolia	Western Australia, *Barrett* RLB 5370 (PERTH)	–	MW589145	KX963552	–
Chaetospora curvifolia	Western Australia, *Verboom* 1240 (BOL)	KF553613	KF553523	–	KF553574
Chaetospora turbinata	New South Wales, Australia, *Bruhl* 2355 (NE)	–	MW589146, MW589147	–	–
Chaetospora turbinata	New South Wales, Australia, *McLaughlin & Wilson* 35 (NE)	–	AY230034	–	–
Chaetospora turbinata	Victoria, *Gibbs* 80a (NE)	–	MW589148	KX963551	–
Gahnia deusta (R.Br.) Benth.	S. Australia, *Alcock* 11198 (WS)	U49231	–	–	–
Gahnia deusta	S. Australia, *Barrett* RLB 5140 (PERTH)	–	MW589149	MW605210	MW588443
Gahnia radula (R.Br.) Benth.	Victoria, *Barrett* RLB 5210 (PERTH)	–	MW589150	MW605211	MW588444
Gahnia radula	Victoria, *Walsh & Barrett* NGW 7003 (MEL)	–	–	–	MW588445
Gahnia trifida Labill.	Western Australia, *Barrett & Moody* RLB 4331 (PERTH)	–	MW589151	MW605212	MW588446
Gahnia trifida	Western Australia, *Verboom* 1228 (BOL)	KF553607	KF553509	–	KF553557
Gahnia tristis Nees ex Hook. & Arn.	Japan, *Hirahara* 20361 (OKAY)	AB369963	MF2568	AB261677	–
Gahnia tristis	*Shaw* 885 (K)	–	KF553510	–	KF553558
Morelotia affinis	New Zealand, *Bruhl et al.* JJB 2923 (NE)	–	MW589152	–	–
Morelotia affinis	New Zealand, *Bruhl et al.* JJB 2924 (NE)	–	MW589153	–	–
Morelotia affinis	New Zealand, *de Lange* 8023 (CHR)	KT626742	–	–	–
Morelotia gahniiformis Gaudich.	Hawaii, *Herbst* 1197 (GENT)	EF178576	–	–	–
Morelotia gahniiformis	Hawaii, *Morden* 2117 (PERTH)	–	KF553519	KF553452	–
Morelotia gahniiformis	Hawaii, *Morden s.n.* HPDL2087 (HAW)	–	MW589154	–	–
Morelotia gahniiformis	Hawaii, *Wood* 3197 (PTBG)	–	MW589155	MW605213	–

Name	Voucher	*rbcL*	*trnL-F*	ITS	ETS
Morelotia microcarpa (S.T.Blake) R.L.Barrett & K.L.Wilson	Western Australia, *Barrett & Briggs* RLB 5274 (PERTH)	–	MW589156	–	–
Morelotia octandra (Nees) R.L.Barrett & J.J.Bruhl	Western Australia, *Barrett* RLB 5050A (PERTH)	–	MK511364	–	–
Morelotia octandra	Western Australia, *Hodgon & Bruhl* JH 795 (NE)	–	MW589157	–	–
Morelotia octandra	Western Australia, *Hodgon & Bruhl* JH 809 (NE)	–	MW589158	–	–
Morelotia octandra	Western Australia, *Verboom* 1242 (BOL)	KF553627	KF553531	–	–
Tetraria arundinacea (Sol. ex Vahl) T.Koyama	New Caledonia, *Wilson* 9935 (NSW)	–	AY230036	–	–
Tetraria breviseta (J.Raynal) Larridon	New Caledonia, *Bruhl* JJB 3261 (NE)	–	MF314972	–	–
Tetraria bromoides (Lam.) H.Pfeiff.	S. Africa, *Verboom* 641 (BOL)	–	DQ419851	–	–
Tetraria burmannii (Vahl) C.B.Clarke	S. Africa, *Verboom* 1219 (BOL)	–	KJ545840	–	KJ545771
Tetraria cf. *burmannii*	S. Africa, *Slingsby* 002 (BOL)	–	KJ545835	–	KJ545764
Tetraria capillacea (Thunb.) C.B.Clarke	S. Africa, *Verboom* 1313 (BOL)	–	KJ545842	–	–
Tetraria cernua (Levyns) Larridon	S. Africa, *Verboom* 707 (BOL)	–	KF553506	–	KF553551
Tetraria comosa (C.B.Clarke) T.Koyama	New Caledonia, *Bruhl* JJB 3258 (NE)	–	MH286443	–	–
Tetraria comosa	New Caledonia, *Wilson & Jaffre* 7673 (GENT)	–	MF314973	–	–
Tetraria compressa Turrill	S. Africa, *Verboom* 653 (BOL)	KJ613587	DQ419854	–	KJ545785, KJ613578
Tetraria crinifolia (Nees) C.B.Clarke	S. Africa, *Verboom* 638 (BOL)	DQ058348, KJ545814	DQ058309	–	–
Tetraria eximia C.B.Clarke	S. Africa, *Verboom* 647 (BOL)	KJ545817	KJ545847	–	KJ545783
Tetraria cf. *eximia*	S. Africa, *Verboom* 720 (BOL)	–	–	–	KJ545789
Tetraria cf. *eximia*	S. Africa, *Verboom* 891 (BOL)	–	KJ545850	–	–
Tetraria fasciata (Rottb.) C.B.Clarke	S. Africa, *Verboom* 639 (BOL)	–	KJ545846	–	KJ545779
Tetraria cf. *fasciata*	S. Africa, *Verboom* 644 (BOL)	–	DQ419858	–	KJ545782
Tetraria ferruginea C.B.Clarke	S. Africa, *Verboom* 527 (BOL)	–	KJ545843	–	KJ545776
Tetraria fimbriolata (Nees) C.B.Clarke	S. Africa, *Verboom* 533 (BOL)	–	DQ419862	–	KJ545777
Tetraria flexuosa (Thunb.) C.B.Clarke	S. Africa, *Verboom* 505 (BOL)	–	DQ419859	–	KJ613579, KF553587
Tetraria flexuosa	S. Africa, *Verboom* 733 (BOL)	–	DQ419860	–	KJ545790
Tetraria cf. *flexuosa*	S. Africa, *Kennedy* A (BOL)	–	–	–	KJ545766
Tetraria fourcadei Turrill & Schönland	S. Africa, *Verboom* 633 (BOL)	–	KJ545845	–	KJ545783
Tetraria involucrata (Rottb.) C.B.Clarke	S. Africa, *Verboom* 1283 (BOL)	–	–	–	KF553588
Tetraria involucrata	S. Africa, *Verboom* 661 (BOL)	KF553621	DQ419852	–	KJ545787
Tetraria maculata Schönland & Turrill	S. Africa, *Verboom* 528 (BOL)	–	KJ545844	–	–
Tetraria cf. *maculata*	S. Africa, *Verboom* 763 (BOL)	–	KJ545849	–	–
Tetraria microstachys (Vahl) H.Pfeiff.	S. Africa, *Verboom* 640 (BOL)	DQOS8347, KJ545815	DQ058307	–	KF553589, KJ545780
Tetraria cf. *microstachys*	S. Africa, *Verboom* 513 (BOL)	–	DQ419856	–	KJ545775

Name	Voucher	*rbcL*	*trnL-F*	ITS	ETS
Tetraria nigrovaginata (Nees) C.B.Clarke	S. Africa, *Verboom* 500 (BOL)	–	DQ419857	–	KJ545773, KF553590
Tetraria pubescens Schönland & Turrill	S. Africa, *Verboom* 651 (BOL)	–	DQ419855	–	–
Tetraria cf. *pubescens*	S. Africa, *Verboom* 1280 (BOL)	–	KJ545839	–	KJ545770
Tetraria pygmaea Levyns	S. Africa, *Slingsby* pygsil (BOL)	–	KJ545837	–	KJ545768
Tetraria pygmaea	S. Africa, *Verboom* 1276 (BOL)	–	KJ545838	–	KJ545769
Tetraria cf. *pygmaea*	S. Africa, *Verboom* 1304 (BOL)	–	KJ545841	–	KJ545772
Tetraria raynaliana Larridon	New Caledonia, *Wilson & Jaffre* 7672 (NSW)	–	MF314985	–	–
Tetraria raynaliana	New Caledonia, *Wilson* 9940 (NSW)	–	AY230037	–	–
Tetraria secans C.B.Clarke	S. Africa, *Verboom* 658 (BOL)	KJ545818	KJ545848	–	KJ545786
Tetraria cf. *secans*	S. Africa, *Verboom* 896 (BOL)	–	KJ545851	–	KJ545791
Tetraria setacea (J.Raynal) Larridon	New Caledonia, *McKee* 30273 (P)	–	MF314987	–	–
Tetraria spiralis C.B.Clarke	S. Africa, *Verboom* 719 (BOL)	–	–	–	KJ545788
Tetraria stagnalis (Däniker) T.Koyama	New Caledonia, *Wilson & Jaffre* 7756 (NSW)	–	MF314988	–	–
Tetraria sylvestris (J.Raynal) Larridon	New Caledonia, *McKee* 28051 (P)	–	MF314989	–	–
Tetraria thermalis (L.) C.B.Clarke	S. Africa, *Verboom* 643 (BOL)	KJ613588	DQ058308	–	KJ545781
Tetraria triangularis (Boeckeler) C.B.Clarke	S. Africa, *Britton* 302 (BOL)	–	–	–	KJ613571
Tetraria triangularis	S. Africa, *Britton* 303 (BOL)	–	KJ613554	–	KJ613570
Tetraria triangularis	S. Africa, *Britton* 310 (BOL)	–	–	–	KJ613569
Tetraria triangularis	S. Africa, *Britton* 313 (BOL)	–	–	–	KJ613565
Tetraria triangularis	S. Africa, *Britton* 321 (BOL)	KJ613583	KJ613548	–	–
Tetraria triangularis	S. Africa, *Britton* 322 (BOL)	–	–	–	KJ613566
Tetraria triangularis	S. Africa, *Britton* 343 (BOL)	–	KJ613558	–	KJ613573
Tetraria triangularis	S. Africa, *Britton* 348 (BOL)	–	–	–	KJ613575
Tetraria triangularis	S. Africa, *Britton* 353 (BOL)	–	KJ613561	–	–
Tetraria triangularis	S. Africa, *Britton* 354 (BOL)	KJ613585	KJ613559	–	KJ613574
Tetraria triangularis	S. Africa, *Britton* 359 (BOL)	–	KJ613562	–	KJ613577
Tetraria triangularis	S. Africa, *Verboom* 518 (BOL)	–	DQ419853	–	–
Tetraria triangularis	S. Africa, *Verboom* 782 (PRE)	–	KJ613564	–	–
Tetraria ustulata (L.) C.B.Clarke	S. Africa, *Verboom* 501 (BOL)	KF553625	DQ419861	–	–
Tetraria ustulata	S. Africa, *Verboom* 664 (BOL)	–	–	–	KF553594
Tetraria cf. *ustulata*	S. Africa, *Helme* A (BOL)	–	KJ545836	–	KJ545765
Tetraria wallichiana C.B.Clarke	S. Africa, *Kennedy* B (BOL)	–	–	–	KF545767
Tricostularia aphylla (R.Br.) K.L.Wilson & R.L.Barrett	Western Australia, *Barrett* RLB 2753 (PERTH)	–	MK511365	–	–
Tricostularia aphylla	Western Australia, *Keighery & Gibson* 5082 (PERTH)	–	MK511366	–	MW588447
Tricostularia compressa Nees ex Lehm.	Western Australia, *Davis* 1721 (PERTH)	–	MW589159	MW605214	MW588448
Tricostularia compressa	Western Australia, *Hislop* 2537 (PERTH)	–	MW589160	MW605215	MW588449
Tricostularia compressa	Western Australia, *Hodgon & Bruhl* 812 (NE)	–	MW589167	–	–

Name	Voucher	*rbcL*	*trnL-F*	ITS	ETS
Tricostularia drummondii (Steud.) R.L.Barrett & K.L.Wilson	Western Australia, *Gibson* 4035 (PERTH)	–	MW589161	MW605216	MW588450
Tricostularia exsul (C.B.Clarke) K.L.Wilson & R.L.Barrett	Western Australia, *Barrett* RLB 5020 (PERTH)	–	–	KX963565	–
Tricostularia neesii Lehm.	Western Australia, *Barrett & Briggs* RLB 5302 (PERTH)	–	MW589162	MW605217	MW588451
Tricostularia neesii	Western Australia, *Pryde & Morley* 12 (PERTH)	–	–	–	MW588452
Tricostularia newbeyi	Western Australia, *Byrne* 2545 (PERTH)	–	MW589163	MW605218	MW588453
Tricostularia newbeyi	Western Australia, *Edinger & Marsh* DJE 4094 (PERTH)	–	–	–	MW588454
Tricostularia pauciflora (F.Muell.) Benth.	New South Wales, Australia, *Wilson* 9910 (NSW)	AY725954	AY230038	–	–
Tricostularia pauciflora	New South Wales, *Gibbs et al*. AKG 53 (NE)	–	MW589164	–	KF553597
Tricostularia pauciflora	Victoria, *Gibbs & Fitzgerald* AKG 88 (NE)	–	MW589165	–	–
Tricostularia sandifordiana R.L.Barrett & K.L.Wilson	Western Australia, *Barrett & Gaskell* RLB 5045 (PERTH)	–	MK511369	MW605219	MW588455
Tricostularia sp. Albany (R.L. Barrett & K.L. Wilson RLB 5342)	Western Australia, *Barrett & Wilson* RLB 5342 (PERTH)	–	MW589166	MW605220	MW588456
Tricostularia sp. Albany	Western Australia, *Barrett et al*. RLB 4389 (PERTH)	–	MK511367	MW605221	MW588457
Xyroschoenus hornei (C.B.Clarke) Larridon	Seychelles, *Senterre & Henriette* 7107 (GENT)	–	MF314975	–	MF315012

Laboratory work was conducted at Kings Park & Botanic Garden, Western Australia, and the Jodrell Laboratory, Kew, UK, using slightly different methods. DNA extraction at KPBG followed a modified protocol from Carlson *et al.* (1991) and Csaikl *et al.* (1998). About half a gram of plant material was ground using a mortar and pestle with acid-washed sand in liquid nitrogen until a powder was obtained. One mL of Carlson extraction buffer (Csaikl *et al.* 1998) was added and the liquid transferred to a 1.5 mL Eppendorf tube, to which 0.4 µg RNase A (Qiagen, Hilden, Germany) was added before the samples were incubated in a water bath at 65°C for 15 mins. Samples were then centrifuged at 11,500 rpm for 10 min. The supernatant was transferred to a new 1.5 mL Eppendorf tube and 600 µL of chloroform: isoamyl alcohol (24:1) was added to each sample. Samples were then gently shaken for 30 min. before being centrifuged at 9,000 rpm for 10 min. The supernatant was transferred to a new 1.5 mL Eppendorf tube and an equal volume (approx. 650 µL) of cold isopropanol was added to each sample. This was mixed gently by inversion before the samples were stored in a -20°C freezer for 20 min. Samples were centrifuged at 10,000 rpm for 10 mins before the liquid component was discarded. One mL cold 70% ethanol was added to each sample before they were centrifuged at 13,000 rpm for 10 min. The liquid component was discarded and the samples were air dried for at least two hours. The DNA was re-suspended in 80 µL TE buffer (0.1 M).

At the Jodrell Laboratory, Royal Botanic Gardens, Kew, DNA extractions were performed using 0.2–0.3 g silica dried leaves and a modified version of the 2X CTAB method of Doyle and Doyle (1987). Before precipitation, an aliquot was purified using QIAgen PCR purification kit (QIAgen, Crawley, West Sussex, UK) following the manufacturer's protocols. The total DNA was further purified for long-term storage in the DNA Bank at RBG Kew using a caesium chloride/ethidium bromide gradient (1.55g/ml) followed by a dialysis procedure.

DNA amplification

At Kings Park, DNA was amplified using polymerase chain reaction (PCR) with a total volume of 50 µL. Each PCR contained 10 µL 5× polymerisation buffer (Fisher Biotech, Subiaco, WA, Australia), and a final concentration of 2 mM $MgCl_2$ (Fisher Biotech), 0.12% DMSO (Merck, Kilsyth, VIC, Australia), 0.06% BSA (Sigma Aldrich, St Louis, MO, USA), 5 µM each of the forward and reverse primers, and 0.2 U Taq DNA polymerase (Fisher Biotech). Primers used are listed in Table 4 (note that no new *rbcL* data was generated).

Table 4. Primers used to amplify DNA for sequencing.

Region	Primer	Reference
ETS1-F	CTGTGGCGTCGCATGAGTTG	Starr *et al*. 2003
18S-R	AGACAAGCATATGACTACTGGCAGG	Starr *et al*. 2003
ITS1	GCATATCAATAAGCGGAGGA	White *et al*. 1990
ITS4	TCCTCCGCTTATTGATATGC	White *et al*. 1990
*trn*Lc	CGAAATCGGTAGACGCTACG	Taberlet *et al*. 1991
*trn*Ld	GGGGATAGAGGGACTTGAAC	Taberlet *et al*. 1991
*trn*Le	GGTTCAAGTCCCTCTATCCC	Taberlet *et al*. 1991
*trn*Ff	ATTTGAACTGGTGACACGAG	Taberlet *et al*. 1991

PCRs were variously run on GeneAmp (Applied Biosystems, Foster City, CA, USA) or Palm-Cycler (Corbett Life Science, Concord, NSW, Australia) thermal cyclers using the following cycle for ETS: Hold: 95°C for 90 s, then 35 cycles of: 95°C for 30 s; 50°C for 60 s; 72°C for 90 s; hold 72°C for seven mins and finally hold indefinitely at 4°C. The PCR products were purified using AMPure beads (Agencourt Bioscience, Beverley, Massachusetts, USA).

At the Jodrell Laboratory, cycle sequencing reactions were carried out using the BigDye Terminator Mix (Applied Biosystems, ABI, Warrington, Cheshire, UK). Products were run on an ABI 3100 Genetic Analyser or an ABI 377 automated sequencer according to the manufacturer's protocols. Both strands were sequenced for each region. Additional sequencing was variously performed at AGRF (Brisbane, Australia), or by Macrogen Inc. (Seoul, Republic of Korea).

Phylogenetic analyses

A phylogeny of the *Tricostularia* clade has been reconstructed here using the external transcribed spacer (ETS) and internal transcribed spacer (ITS) regions of nrDNA, *rbcL* gene and the *trnL* intron and *trnL–F* spacer of cpDNA. Sequences were edited using CodonCode Aligner software (CodonCode Corp., Dedham, Massachusetts, USA) and checked with BLAST (http://blast.ncbi.nlm.nih.gov/Blast.cgi) to ensure that the sequences produced were not from a contaminated source. Sequences were then manually aligned in Geneious (ver. 9.1.7, see https://www.geneious.com, accessed April 2018). Phylogenetic analyses were performed using Bayesian inference implemented in MrBayes (ver. 3.2.6, see https://github.com/NBISweden/MrBayes/releases/tag/v3.2.6; Huelsenbeck and Ronquist 2001; Ronquist *et al*. 2012). *Gahnia deusta* (R.Br.) Benth. was designated as outgroup for all analyses, with two samples of this and three additional *Gahnia* species included to minimise long-branch attraction to the outgroup. Four Markov-Chain Monte Carlo (MCMC) chains were run for 1.5 million generations, with one tree sampled every 250 generations at a temperature of 0.2 with default priors (gamma), and GTR substitution model, GTR+G being consistent with the analyses of Semmouri *et al*. (2019) using the same markers within Cyperaceae. Subsequent analyses were performed using the optimal models GTR+I+G for ETS and HKY+I for *rbc*L (identified by the Akaike Information Criterion corrected for small sample sizes in jModelTest; Posada 2008) and these models were also applied to the concatenated analysis, but no significant diffrences in topology or support values were identified. The first 200,000 trees recovered were discarded as burn-in (trees produced before convergence).

Results

The sequence data comprised 67 sequences for ETS, 19 for ITS, 20 for *rbcL* and 91 for *trnL-F*, each including up to 8 outgroup samples (all *Gahnia* species; see Table 3). Alignment and character statistics are shown in Table 5. As no well-supported conflicts among the different markers were found, a reduced concatenated dataset (supermatrix) of 58 samples, including 6 outgroup samples, was constructed to test support for the backbone nodes based on all four sequence regions. In most cases, a single sample was used for all sequence regions, but in a few cases, samples were pooled in the concatenated analysis where specific regions were otherwise missing from the supermatrix. Most samples are represented by at least two markers in the supermatrix, but to ensure the diversity of the subtribe was represented in the phylogeny, several important samples were included on the basis of single available markers only.

Table 5. Descriptive statistics for individual and concatenated marker alignments.

	ETS	ITS	*trnL-F*	Concatenated (with 20 *rbcL* sequences)
Number of samples (new)	67 (16)	19 (12)	91 (22)	55 (–)
Sequence length range (bp)	415–555	421–679	376–987	603–3,202
Aligned length (bp)	556	690	989	3,295
GC content (%)	59.7	66.8	28.1	40.4
Variable sites	489	225	628	2,099
Missing sequences	–	–	–	94/220 (43%)
Gaps + missing characters (%)	8.3	7.5	11.3	36.3

Phylogeny based on concatenated data

The monophyly of five of the six genera recognised here is supported with posterior probability (PP) of 1 or 0.99 in our concatenated analysis. *Xyroschoenus* is only represented by a single sample on a long branch, and it is weakly placed as sister to *Morelotia* (Figure 1).

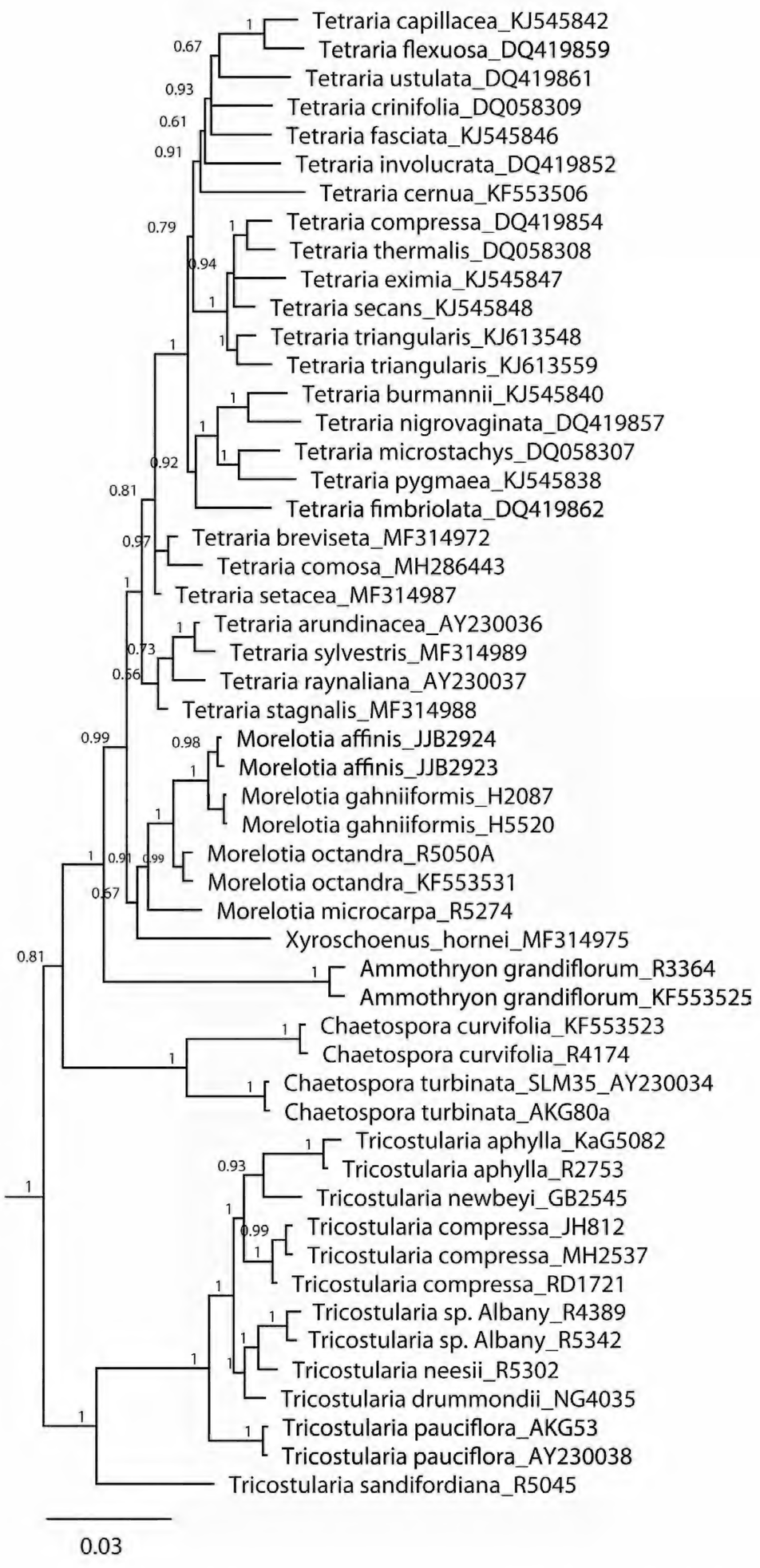

Fig. 1. Phylogeny of selected Schoeneae inferred from concatenation of *rbcL* and *trnL-F* (cpDNA), ITS and ETS (nrDNA) data. Posterior output from MrBayes. Numbers above lines are posterior probability. *Gahnia deusta* was designated as outgroup; *G. trifida* and *G. tristis* were also included to reduce long-branch attraction to the outgroup (not shown due to long branch-lengths).

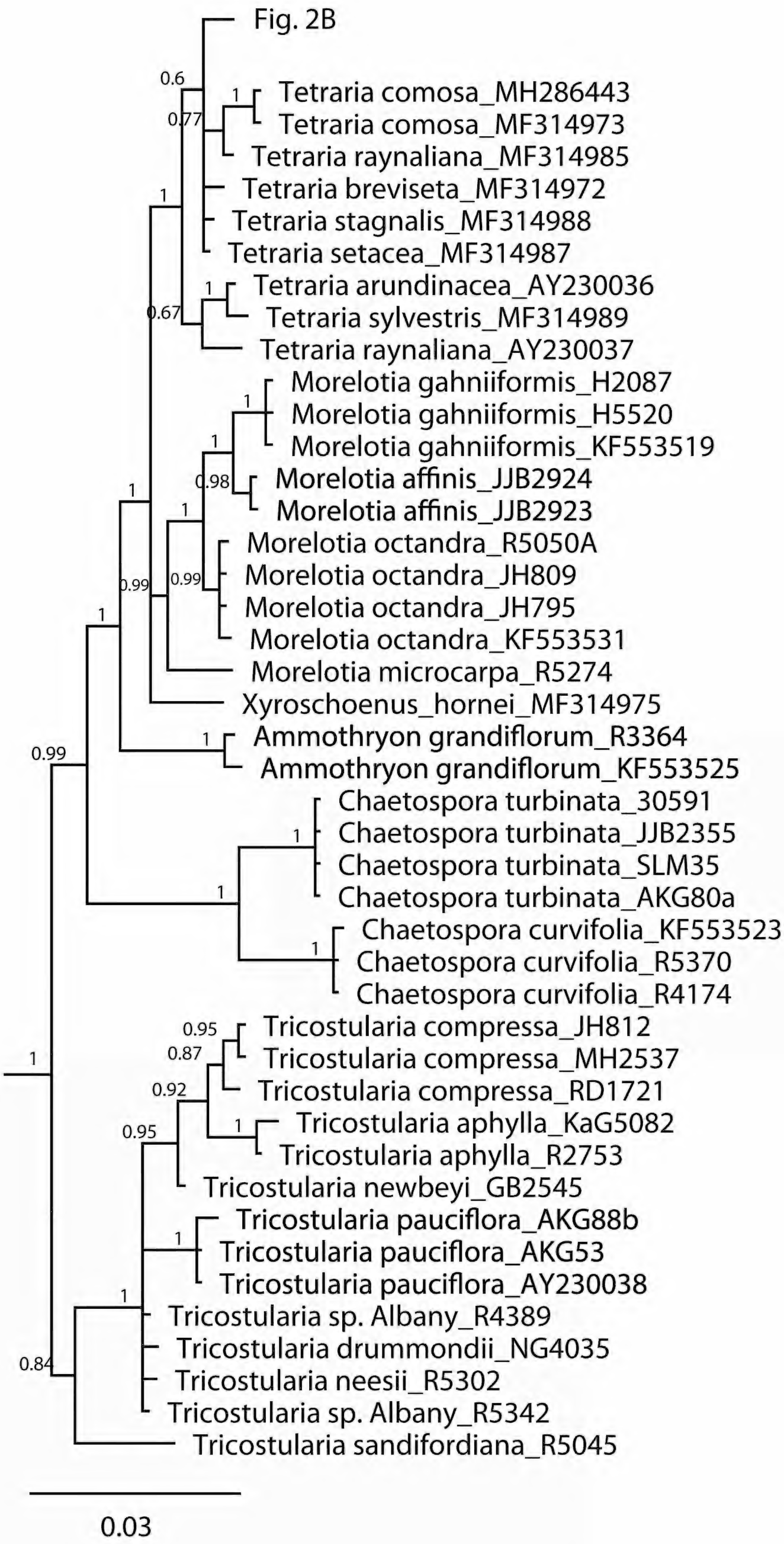

Fig. 2A. Phylogeny of selected Schoeneae inferred from *trnL* intron and *trnL–F* spacer data (cpDNA). Posterior output from MrBayes. Numbers above lines are posterior probability. *Gahnia deusta* was designated as outgroup; *G. radula*, *G. trifida* and *G. tristis* were also included to reduce long-branch attraction to the outgroup (not shown due to long branch-length).

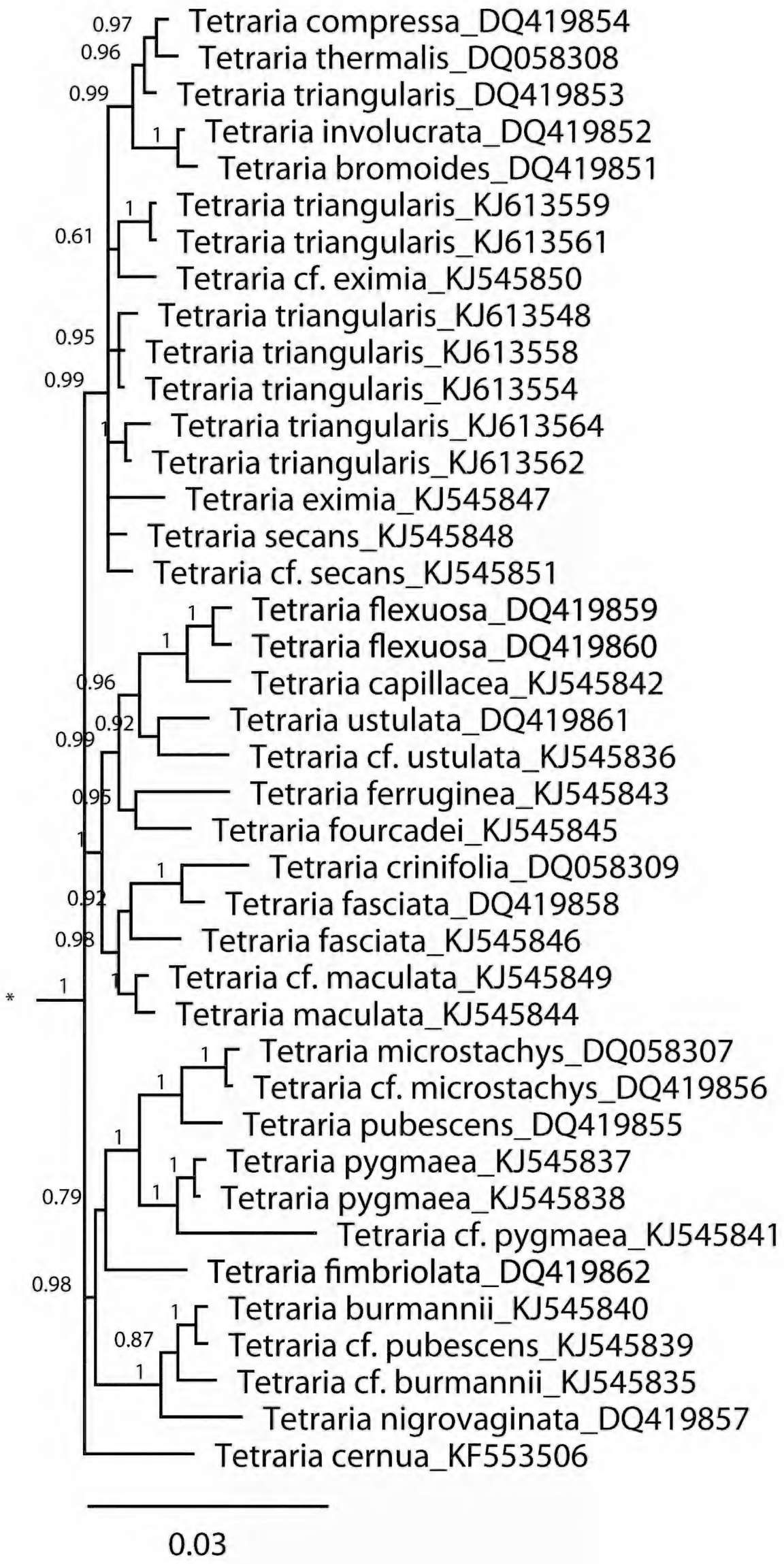

Fig. 2B. Phylogeny of selected Schoeneae inferred from *trnL* intron and *trnL–F* spacer data (cpDNA). Posterior output from MrBayes. Numbers above lines are posterior probability. *Gahnia deusta* was designated as outgroup; *G. radula*, *G. trifida* and *G. tristis* were also included to reduce long-branch attraction to the outgroup (not shown due to long branch-length).

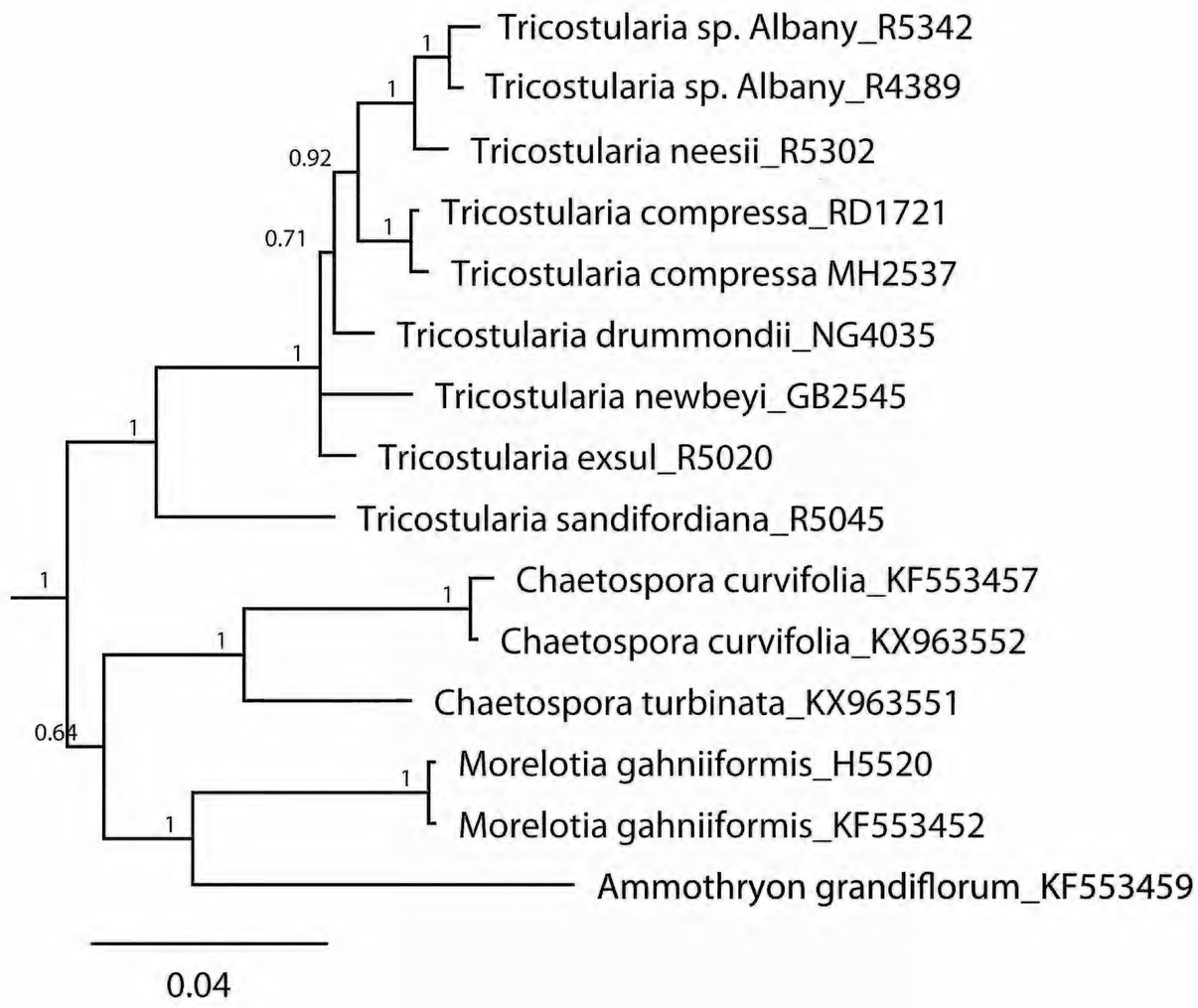

Fig. 3. Phylogeny of selected Schoeneae inferred from ITS data (nrDNA). Posterior output from MrBayes. Numbers above lines are posterior probability. *Gahnia deusta* was designated as outgroup; *G. radula*, *G. trifida* and *G. tristis* were also included to reduce long-branch attraction to the outgroup (not shown due to long branch-length).

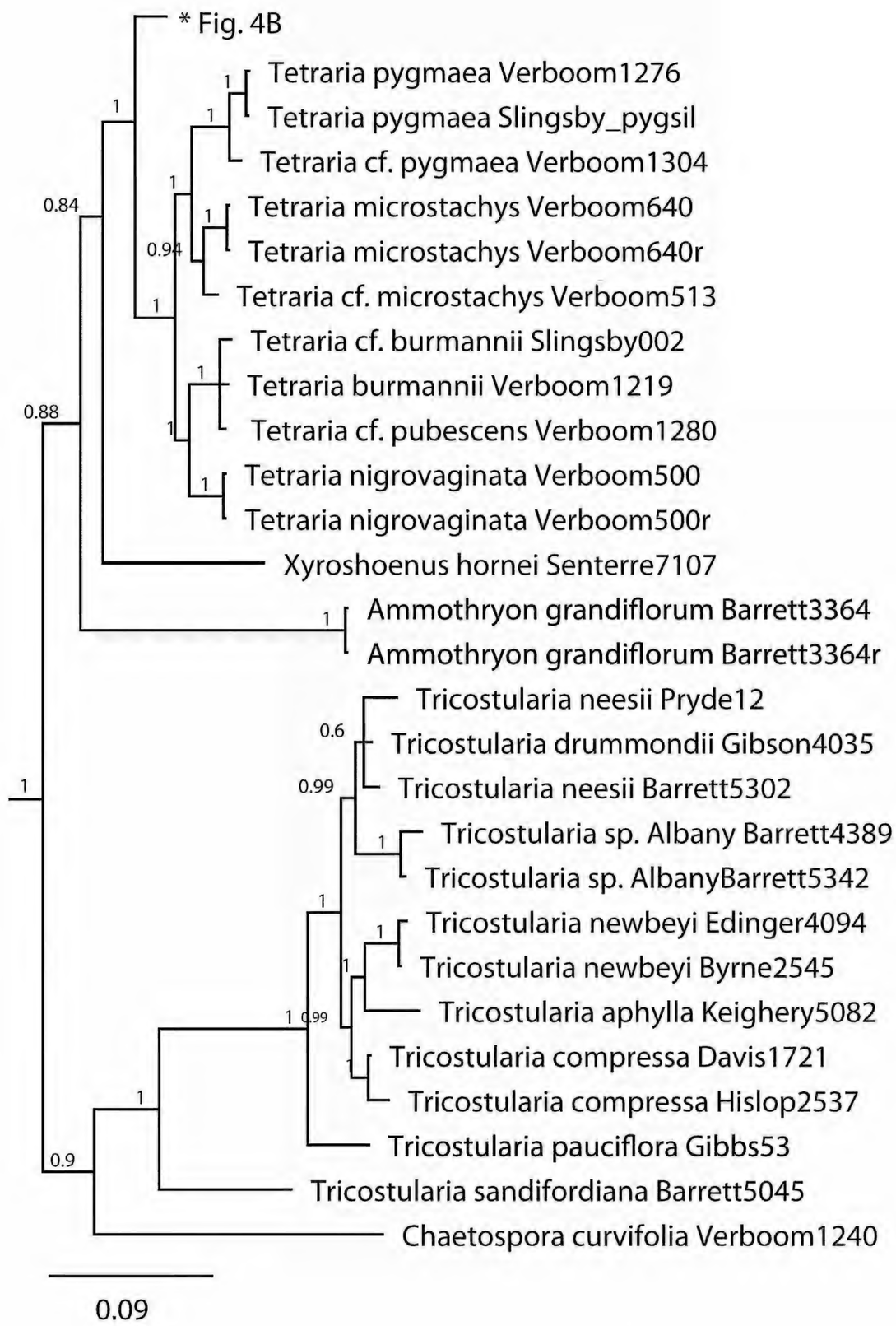

Fig. 4A. Phylogeny of selected Schoeneae inferred from ETS data (nrDNA). Posterior output from MrBayes. Numbers above lines are posterior probability. *Gahnia deusta* was designated as outgroup; *G. radula*, *G. trifida* and *G. tristis* were also included to reduce long-branch attraction to the outgroup (not shown due to long branch-length).

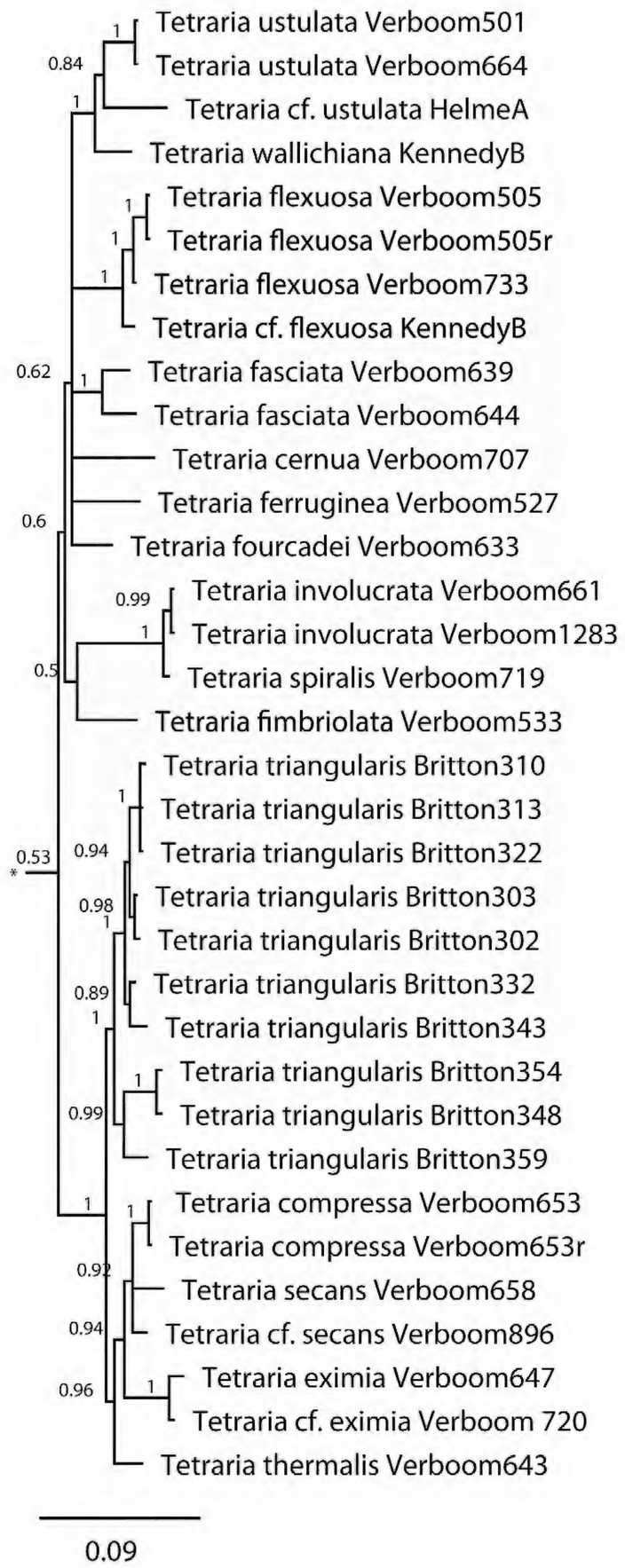

Fig. 4B. Phylogeny of selected Schoeneae inferred from ETS data (nrDNA). Posterior output from MrBayes. Numbers above lines are posterior probability. *Gahnia deusta* was designated as outgroup; *G. radula*, *G. trifida* and *G. tristis* were also included to reduce long-branch attraction to the outgroup (not shown due to long branch-length).

Tricostularia (excluding *Anthelepis*) is strongly supported as a monophyletic genus (PP 1), sister to the remainder of the Tricostulariinae (PP 0.81; Figure 1). *Tricostularia sandifordiana*, a species whose generic placement has been questioned due to its gross morphology resembling species of Restionaceae, is strongly supported as sister to all other *Tricostularia* species (PP 1). The inclusion in *Tricostularia* of *Tricostularia aphylla* and *T. exsul* is strongly supported (PP 1); these two species were transferred from *Lepidosperma* Labill. by Barrett and Wilson (2012).

Chaetospora, recently reinstated and redefined by Barrett *et al.* (2020) to include three southern Australian species, is also strongly supported as monophyletic (PP 1) and is possibly the next-diverging lineage in Tricostulariinae, but this relationship is not supported by our analyses (P 0.81; Figure 1).

Ammothryon grandiflorum is fully supported as sister to a clade containing *Xyroschoenus*, *Morelotia* and *Tetraria* (PP 1; Figure 1).

The monotypic, geographically isolated and morphologically distinctive *Xyroschoenus*, endemic to the Seychelles (Larridon *et al.* 2018a), is possibly sister to *Morelotia* in our analyses but this relationship is not supported (P 0.67).

A key finding is the placement of *Tetraria microcarpa* (not previously sequenced), strongly supported as sister to both *Tetraria* (*Tetrariopsis*) *octandra* and *Morelotia* (PP 0.98). *Morelotia* in its traditional circumscription (*M. affinis* and *M. gahniiformis*) is fully supported as monophyletic (PP 1).

Tetraria (*sensu* Larridon *et al.* 2018b) is strongly supported as monophyletic (PP 1). A number of the internal nodes remain poorly supported, especially for the New Caledonian taxa; however, they are only represented by *trnL-F* data.

Discussion

Analysis of nuclear data generated with the Angiosperms353 bait kit, including near-complete generic representation across Cyperaceae, has resolved tribe Schoeneae as monophyletic, with strong support for eight internal clades (Larridon *et al.* 2021b). These eight clades will be recognised as subtribes to facilitate analysis and discussion of the extensive morphological diversity found within the tribe, especially given significant confusion over past generic delimitation (Slingsby and Verboom 2006; Bruhl *et al.* 2008a, 2008b; Wilson *et al.* 2012; Viljoen *et al.* 2013; Muasya 2016; Musili *et al.* 2016; Barrett *et al.* 2017, 2019, 2020a, 2020b; Larridon *et. al.* 2018a, 2018b, 2019; Semmouri *et al.* 2019). The subtribe Tricostulariinae is formally described here so that a valid subtribal name is available.

The molecular data and analyses presented here provide evidence for a narrowed circumscription of the genus *Tricostularia*. Several species traditionally included in *Tricostularia* are now excluded from the genus and we return to the concept of Kükenthal (1944). *Tricostularia guillauminii* (Kük.) J.Raynal, *Tricostularia paludosa* (R.Br.) Benth. and *Tricostularia undulata* (Thwaites) J.Kern have been placed in the new genus *Anthelepis* R.L.Barrett, K.L.Wilson & J.J.Bruhl (Barrett *et al.* 2019). With the exclusion of these species, *Tricostularia* forms a well-supported monophyletic group. The morphologically anomalous *Tricostularia sandifordiana* is on a long branch relative to other species, but recognition of an additional genus does not appear justified on morphological grounds.

It is evident that current species concepts are variously monophyletic, polyphyletic or paraphyletic, which, in combination with expressed morphological diversity, suggests that additional species need to be recognised. Additional sampling is required to determine the relationships among all of the morphotypes observable in herbarium collections and to determine the extent of genetic variation within each taxon.

The genus *Tricostularia* as defined here is characterised by culms commonly noded with leaf lamina usually reduced to bracts. The inflorescence is small and spike- or head-like. There is considerable morphological variation in specimens historically assigned to *Tricostularia compressa* and *T. neesii* and new species are recognised here. A number of the morphotypes currently held at NSW and PERTH are poorly represented and a full taxonomic revision will require additional fieldwork to assess taxonomic boundaries in some taxa.

There is considerable genetic divergence between the western species *Chaetospora curvifolia* and the eastern species *C. turbinata* (*C. subbulbosa* has not been sequenced, but is expected to be sister to *C. curvifolia* based on morphological similarity and geographic distribution).

Ammothryon grandiflorum, long included in the genus *Schoenus* as a morphologically anomalous species (Mueller 1875; Rye 1987; Wheeler and Graham 2002), is strongly supported as sister to the *Xyroschoenus–Morelotia–Tetraria* clade, justifying its recognition here as a new, monotypic genus which also finally renders *Schoenus* monophyletic (see Elliott *et al.* 2021).

Based largely on biogeography, it had been expected that *Tetraria microcarpa* and *Tetrariopsis octandra* would form a clade sister to *Morelotia*. Bruhl (1995) first recovered *Morelotia* and *Tetrariopsis* as sister taxa based on morphology. The results here, based on molecular data, raise the question whether the two should be united in one genus. *Tetraria microcarpa* is here resolved as sister to both *Tetrariopsis* and *Morelotia*, so the only alternative to create monophyletic lineages would be the description of *Tetraria microcarpa* as a distinct genus. We do not consider that warranted on morphological grounds, the key difference of that species being an overall reduction in size rather than morphological synapomorphies. Larridon *et al.* (2018a) continued to distinguish *Morelotia* and *Tetrariopsis*, and provided a key to differences; 8 stamens (3–)4(–5) style branches, and mature fruit deciduous for *Tetrariopsis octandra*, *vs* 3 stamens, 3 style branches, and fruit persistently attached by old style filaments for *Morelotia*. However, on closer morphological study of the three Western Australian species, and the addition of *Morelotia involuta* from Rapa Iti (Barrett *et al.* 2021b), these differences do not hold. We conclude that a single genus is the best option to accommodate the six species of this clade within the generic classification of the Tricostulariinae, given the level of morphological variation they express. We choose to expand the definition of the genus *Morelotia* to include *Tetraria australiensis*, *T. microcarpa* and *T. octandra*.

We here present the first generic description of the genus *Tetraria* based on the circumscription outlined by Larridon *et al.* (2018b). Additional markers should be generated to resolve relationships within *Tetraria* and to improve our understanding of long-distance dispersal patterns within the genus.

Taxonomy

Tricostulariinae R.L.Barrett, K.L.Wilson & J.J.Bruhl, *subtribus nov*.

Type genus: *Tricostularia* Nees ex Lehm.

Diagnostic characters: Distinguished from other clades in tribe Schoeneae by the following combination of characters: Tufted, rhizomatous, perennial graminoids; leaves basal and commonly cauline, sometimes on an erect caudex (*Ammothryon*, some *Tetraria* and *Xyroschoenus*); culms trigonous or terete; leaf laminas well-developed or much reduced; eligulate; leaf margins scaberulous to denticulate, flat to channelled, sometimes V- or M-shaped in section, sometimes involute or revolute; inflorescence terminal, panicle-like, sometimes appearing head-like (*Chaetospora*, some *Tricostularia*) or spike-like (some *Tricostularia*); spikelet prophyll present at base of spikelets (except *Ammothryon*), glumes distichous, mostly persistent (deciduous in *Tricostularia*); rachilla mostly non-flexuous, straight (elongate and curved around nutlet in *Morelotia affinis*, *M. gahniiformis*, *M. octandra* and *Xyroschoenus*); flowers subtended by upper glumes (except upper glume reduced and infertile in Pacific species of *Morelotia*); lower flower(s) variously bisexual fertile, functionally male or bisexual sterile, upper bisexual or functionally male (*Morelotia octandra*); upper glumes longer than lower; spikelets ranging from few to many in spikelet clusters; perianth absent or bristles 2, 6, or 7–8, shorter or longer than the nutlet; mostly 3 stamens [(3)6 in *Morelotia australiensis*, (4, 6)8(9) in *M. octandra*], stigma mostly 3-fid (3- or 4-fid in some species of *Tetraria*, 3–5-fid in *Morelotia octandra*); nutlets ranging in shape from ovoid to broad ellipsoid or globose.

Constituent genera: *Ammothryon* R.L.Barrett, K.L.Wilson & J.J.Bruhl (1 sp.), *Chaetospora* R.Br. (3 spp.), *Morelotia* Gaudich. (6 species), *Tetraria* P.Beauv. (*c.* 39 spp.), *Tricostularia* Nees ex Lehm. (*c.* 16 species, several undescribed), and *Xyroschoenus* Larridon (1 sp.).

Morphological diversity: Directly comparable character coding for all or representative species for each genus is presented in Appendix 1.

Distribution: Southern Australia (*Ammothryon*, *Chaetospora*, *Tricostularia*); South-western Australia, New Zealand, French Polynesia, Hawaiian Islands (*Morelotia*); New Caledonia to Borneo and New Guinea, Cape Floristic Region to tropical Africa (*Tetraria*); the Seychelles (*Xyroschoenus*).

Notes: Pollen morphology in the subtribe is poorly known and no representatives were examined by Nagels *et al.* (2009) in their review of the family. Moar and Wilmshurst (2003) in their review of New Zealand Cyperaceae pollen describe the pollen of *Morelotia affinis* as 'similar' to *Gahnia*, but do not provide specific characterisation for the species. Examination by light microscopy under phase contrast of *Tricostularia aphylla* pollen found that it is prolate (or pear-shaped), lacks a distal aperture and has 3 lateral apertures (these being ovate and recessed).

Key to the genera of subtribe *Tricostulariinae*

1. Prophyll below spikelet absent; spikelets 12–22 mm long, with 10–14 glumes and 4 bisexual flowers; perianth absent; anthers 7–10 mm long..... ***Ammothryon***

1. Prophyll below spikelet present; spikelets 2.8–25 mm long, with 4–9 glumes and 1–3 bisexual flowers; perianth present or absent; anthers 0.8–6.5 mm long 2

2. Culms with 5–10 nodes below the inflorescence; caudex present; inflorescence 10–35 cm wide, branches arcuate; rachilla curved around nutlet; perianth segments (6)7 or 8, 5–6 mm long..... ***Xyroschoenus***

2. Culms with 0–5 nodes below the inflorescence; caudex usually absent (present in some *Tetraria* spp.); inflorescence 0.3–10 cm wide, branches erect to spreading (sometimes arcuate in *Tetraria*); rachilla usually not curved around nutlet (curved in some *Morelotia* spp.); perianth segments 0, 2 or 6, 0–5 mm long 3

3. Leaf lamina reduced, usually <1 cm long (rarely up to 7 cm); involucral bracts reduced, bract-like; inflorescence slender or contracted, panicle-like or head-like, 0.8–15 cm long.... ***Tricostularia***

3. Leaf lamina well-developed, 4–100 cm long; involucral bracts leaf-like; inflorescence open, elongate or dense, panicle-like or head-like or subglobular, 0.5–1.5 or 5–70 cm long..... 4

4. Culms without nodes; leaf lamina 0.3–0.9 mm wide; inflorescence head-like or subglobular, 0.5–1.5 cm long; branchlets compact, hidden ..... ***Chaetospora***

4. Culms with 0–5 nodes; leaf lamina (0.5–)1–20 mm wide; inflorescence open, elongate or dense, panicle-like, 5–70 cm long; branchlets obvious, erect to spreading..... 5

5. Nutlets ± sessile (shortly stipitate in *M. microcarpa*, which differs from *Tetraria* in having a glabrous style base) ..... ***Morelotia***

5. Nutlets distinctly stipitate ..... ***Tetraria***

Ammothryon R.L.Barrett, K.L.Wilson & J.J.Bruhl, ***gen. nov.***

Type species: *Ammothryon grandiflorum* (Nees ex Lehm.) R.L.Barrett, K.L.Wilson & J.J.Bruhl (based on *Elynanthus grandiflorus* Nees ex Lehm.).

Perennial tufted herbs, 0.7–1.5 m high; rhizome thick, 10–22 mm diam., sometimes pseudobulbous; roots sand-binding; plants clonal, 0.3–1 m across; caudex present; old leaf sheaths covering the caudex, not breaking apart into fibres with age, pale brown to reddish brown. *Culms* stout, erect, leafy, with 4–7 nodes, obtusely trigonous, 2.5–7 mm diam., somewhat ribbed, usually scabrous but otherwise glabrous, base enlarged. *Leaves* basal and cauline, numerous, reducing in size up the culm, ultimately bract-like; phyllotaxy loosely spirotristichous, sheath scabrous, especially on upper leaves, loose around culm, 20–28(–38) mm long, not broader than the leaf lamina, upper margin with short, thick, brownish hairs, ligule absent; lower leaf lamina (150–)220–460 mm long, 5–15 mm wide, lamina ± linear, flat or usually folded, margins and prominent midrib scabrous, apex gradually attenuate. *Inflorescence* open, panicle-like, narrow, 120–750 mm long, 20–45 mm wide; with 7–14 nodes, bracts leaf-like, exceeding the spikelet clusters; branches spreading, with (1–)3–12 spikelets on peduncles 7–16 mm long, arising in each bract axil; spikelet prophyll absent. *Spikelets* brown, very narrowly ovate, 12–22 mm long, with 10–14 glumes, finely and very shortly hairy, only topmost 2–4 fertile, all bisexual, basal glumes 3–6 mm long; fertile glumes 11–20 m long, glabrescent, acute, becoming acuminate; rachilla compact and not or scarcely sinuous in fruiting spikelets. *Perianth* absent. *Stamens* 3; anther connective 6–11 mm long, linear to subulate; anthers pale yellow, 7–10 mm long, with a glabrous apical appendage 1.0–1.5 mm long. *Style* 16–22 mm long, trifid; base 8–12 mm long, slightly enlarged so continuous with the nutlet, branches 8–10 mm long, hairy. *Nutlet* sessile, subovoid but base contracted, 3.2–3.8 mm long, 1.8–2.2 mm diam., with three white ribs that broaden towards the apex; embryo not examined. Photosynthetic pathway inferred from anatomy to be C_3 (*Fitzgerald NSW 4337*; *Salasoo 4017*; Bruhl and Wilson 2007). 1C = 0.39 pg (*Barrett RLB 7785*; Bureš *et al.* 2013).

Diagnostic characters: Related to *Morelotia* Gaudich., *Xyroschoenus* Larridon and *Tetraria* P.Beauv., but distinguished from all of these genera by the combination of the spikelet prophyll below spikelet apparently absent; spikelets 12–22 mm long, with 10–14 glumes and 4 bisexual flowers; perianth absent; and anthers 7–10 mm long. There are superficial morphological similarities to the larger New Caledonian species of *Tetraria*, including *T. comosa* (C.B.Clarke) T.Koyama and *T. raynaliana* Larridon.

Distribution: A single species endemic southern Western Australia.

Etymology: From the Greek *ammos* (sand) and *thryon* (rush), [neuter] in reference to the habitat of this genus, in sandy heath and woodland.

Notes: Larridon *et al.* (2018a) estimated the crown node of the *Ammothryon* lineage at around 22 Ma.

Kükenthal (1938) placed *Schoenus grandiflorus* in *Schoenus* sect. *Stricti* Benth., next to the eastern Australian species *S. villosus* R.Br., which he readily distinguished by the short rhizome, culms with only 1 or 2 nodes, slender, canaliculate leaves, villose sheath margins, spikelets 8–10 mm long, with 4–5 empty glumes that are dark brown. The similarity is superficial.

Ammothryon grandiflorum (Nees ex Lehm.) R.L.Barrett, K.L.Wilson & J.J.Bruhl, *comb. nov.*

Basionym: *Elynanthus grandiflorus* Nees ex Lehm., *Nov. Stirp. Pug.* 54 (1844). *Schoenus grandiflorus* (Nees ex Lehm.) F.Muell., *Fragm.* 9(73): 30 (1875).

Type citation: 'Crescit in locis arenosis calcareisque haud procul ab ora maritima (Perth). (Herb. Preiss. no. 1781).'

Type: Western Australia: Perth, in locis arenosus calcareisque haud procul a bora maritima [in sandy, calcareous places not far from the coast], 9 June 1840, *L. Preiss* [*Plantae Preissianae* No. 1781] (lectotype (here designated): LD 1732115; isolectotypes: B (2 sheets), BM 000900956, G 00195328, G 00195329, HBG 1522312, L 0042719, L 0042720, MEL 2295791, MEL 2295792, NY 00021817, P 00585272).

Illustrations: Clarke (1909: tab. LXXVIII(5, 6), p. 78); Scott and Negus (2002: fig. 1, p. 27); Wheeler and Graham (2002: fig., p. 296); Barrett and Tay (2015: pl. 1–5, p. 201).

Description: As for the genus. (Figure 5).

Diagnostic characters: As for the genus.

Distribution: Endemic to the South West Botanical Province in Western Australia, in near coastal areas from Kalbarri south and east to Israelite Bay.

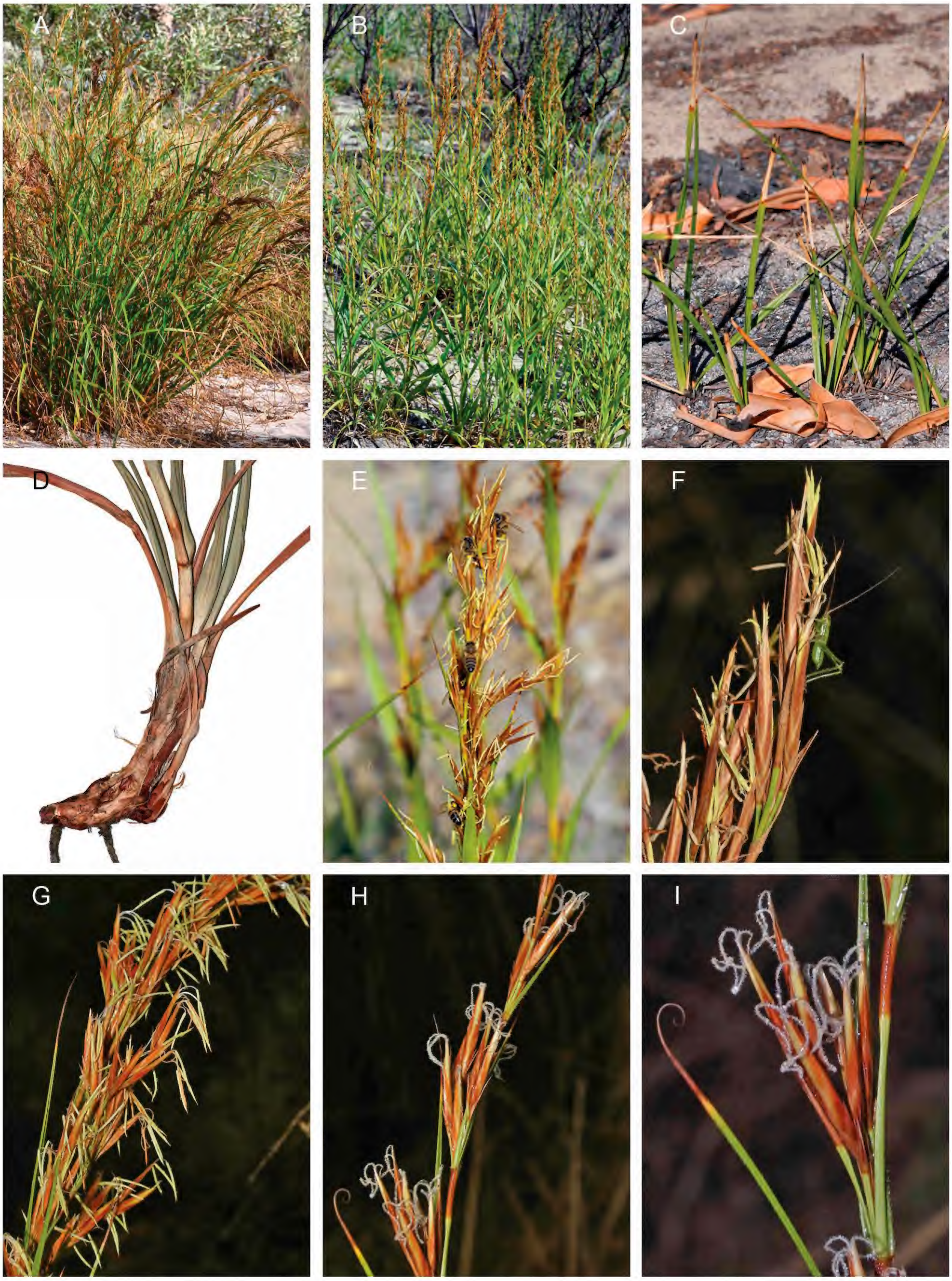

Fig. 5. *Ammothryon grandiflorum*. Kings Park, Perth, Western Australia. A, B. Habit. C. Plants resprouting following fire. D. Plant base showing sand-binding roots, rhizome and leaf bases. E. Staminate inflorescence with honeybees. F. Staminate inflorescence with pollen-feeding katydid. G. Floriferous staminate inflorescence. H. Inflorescence with emergent styles. I. Spikelets with emergent styles. Voucher, *R.L. Barrett 7785* (PERTH). Photos by R.L. Barrett.

Habitat: Occurs close to the coast on sandplains, consolidated sand dunes and limestone in *Banksia* and jarrah-marri woodland, occasionally extending inland along rivers. Recorded in association with *Acacia lasiocarpa*, *A. pulchella*, *Allocasuarina fraseriana*, *A. humilis*, *Anthocercis littorea*, *Banksia attenuata*, *B. ilicifolia*, *B. menziesii*, *B. sessilis* subsp. *sessilis*, *Chaetospora curvifolia*, *Conostephium pendulum*, *Conostylis candicans*, *Corymbia calophylla*, *Eucalyptus marginata*, *Gastrolobium nervosum*, *Gompholobium tomentosum*, *Hibbertia hypericoides*, *H. subvaginata*, *Lepidosperma calcicola*, *L. gladiatum*, *L. scabrum*, *Leucopogon parviflorus*, *Lomandra maritima*, *Macrozamia fraseri*, *Melaleuca systena*, *Mesomelaena pseudostygia*, *Morelotia octandra*, *Schoenus* spp., *Stirlingia latifolia*, *Synaphea spinulosa*, *Templetonia retusa* and *Xanthorrhoea preissii*.

Phenology: Flowers recorded for (March–)April–July. Fruit recorded from July–October.

Selected specimens examined: WESTERN AUSTRALIA: Bold Park, 200 m W of pine plantation, N of Wollaston College, *c.* 8 km W of Perth CBD, 07 June 2006, *R.L. Barrett RLB 3364* (PERTH); corner of Kings Park Road and Thomas Street, 100 m SE of walking track, Kings Park, West Perth, 17 July 2012, *R.L. Barrett RLB 7785* (PERTH); Kalbarri, 5 May 1987, *D. & B. Bellairs 2190* (CANB, PERTH); Cottesloe, near the coast, 25 Aug. 1947, *S.T. Blake 18009* (BRI, CANB, MEL, NSW, PERTH); Denmark wind farm access road, within 50 m of the access gate, 14 Mar. 2017, *G. Byrne 6176* (PERTH); Two Mile Beach, *c.* 6.5 km E of Hopetoun, 28 Sept. 1985, *M. Carter 260* (CANB, PERTH); 5 km S of Cuthbert, 9 Dec. 1996, *R. Davis 1690* (NSW, PERTH); near Perth, Apr. 1901, *W.V. Fitzgerald s.n.* (NSW 74337); N boundary of Reserve A8429 in Leeuwin-Naturaliste National Park (Plot: mr5), 12 Jan. 1990, *N. Gibson & M. Lyons 312* (PERTH); Deep River, Irwins Inlet, Nov. 1912, *S.W. Jackson s.n.* (NSW 74333); Yallingup, 30 Mar 1982, *G.J. Keighery 4543* (CANB, PERTH); Zuytdorp National Park, 0.75 km E from track that parallels coast from State Barrier Fence, on track to Zuytdorp Wreck Site (Site: zu11), 18 Aug. 1995, *G.J. Keighery & N. Gibson 871* (PERTH); 8.9 km S on Moore road from turnoff, 77 km E Geraldton on Geraldton–Mullewa road, 7 Apr. 1992, *K.F. Kenneally 11137* (PERTH); Geraldton, Oct. 1909, *J.H. Maiden s.n.* (NSW 74330); Between Murchison River and Shark Bay, Oct. 1877, *F. Mueller s.n.* (MEL 2202448); 1 km E of Mount Barren, 8 Feb. 1974, *K.R. Newbey 4057* (AD, CANB, MEL, NSW, PERTH); Prevelly Park (Baudin Drive), 10 km W of Margaret River, 30 June 2001, *J. Scott 400* (PERTH); Star Swamp Reserve, Greater Perth, 8 Sept. 2007, *G.A Verboom 1269* (BOL, *n.v.*; PERTH); point at John Cove, Bremer Bay, 16 Dec. 1979, *K.L. Wilson 2915* (NSW, PERTH); 11 km E of Greenhead turn-off on road to Brand Highway and Coorow, 9 Nov. 1994, *K.L. Wilson 8847 & K. Frank* (NE, NSW, PERTH, PRE, SI); Coorow Green Head Road 9.1 km E from junction with Indian Ocean Drive, at Knights Track turn-off, 12 Sep. 2012, *K.L. Wilson 10820 & A. Wilson* (NE, NSW, NY, PERTH); Israelite Bay, *c.* 200 km ENE of Esperance, 19 May 1967, *P.G. Wilson 5862* (NSW, PERTH).

Notes: Perhaps most similar in general appearance to the much smaller *Morelotia octandra*, which is very distinctive in usually having eight anthers (*vs* three), and spikelets 10–15 mm long with 7(–9) glumes (*vs* 12–22 mm long with 10–14 glumes).

A collection at CGE, labelled as *Preiss 134* and the locality given as 'in arenosis Boots Creek ad fluvium Canning' is very similar to the lectotype material and is probably a duplicate of it. The label probably reflects Preiss' field collection number, distributed to Lindley (now in CGE) before Lehmann allocated *Plantae Preissianae* numbers to the collection (see McGillivray 1975; Nordenstam 1980; Crisp 1983; Wilson 1983; Lander 1987; Marchant 1990).

Ammothryon grandiflorum is persistent the landscape due to its clonal growth, with individuals tracked for over 30 years in Kings Park, Perth, and observed to resprout very quickly post-fire (Baird 1977).

This species has the common name of Large Flowered Bog-rush.

Chaetospora R.Br., *Prodr.* 232 (1810), *non* C.Agardh (1824), *non* Faurel & Schotter (1965). *Schoenus* sect. *Chaetospora* (R.Br.) Kuntze in Post & Kuntze, *Lex. Gen. Phan.* 507 (1903).

Type species: *Chaetospora curvifolia* R.Br., designated by Barrett *et al. Telopea* 23: 96 (2020).

=*Ptilanthelium* Steud., *Syn. Pl. Glumac.* 2(8–9): 166 (1855).

Type species: *Ptilanthelium chauvinii* Steud. (= *Chaetospora turbinata* R.Br.).

=*Schoenus* subg. *Pseudomesomelaena* Kük., *Repert. Spec. Nov. Regni Veg.* 44: 180 (1938).

Type species: *Schoenus curvifolius* (R.Br.) Poir. (= *Chaetospora curvifolia* R.Br.), designated by Barrett *et al. Telopea* 23: 96 (2020).

=*Schoenus* sect. *Sphaerocephali* Benth., *Fl. Austral.* 7: 358 (1878) (as *Sphaerocephalae*).

Type species: *Schoenus curvifolius* (R.Br.) Poir. (= *Chaetospora curvifolia* R.Br.), designated by Barrett *et al. Telopea* 23: 96 (2020).

Perennial tufted herbs, 0.1–0.55 m high; plants clonal, usually forming dense tussocks 0.05–0.2 m across; rhizome thin, woody, short, branched, 0.8–3.4 mm diam., pseudobulbous; old leaf sheaths covering the rhizome, usually breaking apart into fine fibres with age, straw-coloured to reddish brown; roots sand-binding or not. *Culms* slender, rigid, erect, 11–53 cm tall, 0.6–2.5 mm broad, not noded, terete to compressed, usually sulcate when dried, smooth, glabrous, green to yellow-green, base not enlarged. *Leaves* all basal, numerous; phyllotaxy loosely spirotristichous; phyllotaxy loosely spirotristichous; sheath 20–70 mm long, 0.7–2.7 mm wide, broader than the leaf lamina, glabrous or scabrid, straw-coloured to reddish-brown, dull, upper margin membranous, oblique, ligule absent; cauline sheath tight around culm; *pseudopetiole* obscure or absent; leaves with a well-developed lamina, not exceeding the culms, lamina dorsiventral, 4–21 cm long, 0.3–0.9 mm wide; bases white or brown-membranous, sometimes dividing; lamina ± linear, flat to channelled above, ± flexuous, old leaf tips usually curling, finely multi-striate, glabrous except for margins, green to brown, concolorous, keeled along mid-nerve or not, margins scaberulous, not recurved, apex long-attenuate, setaceous; lowest leaves reduced to a sheath, lamina reduced to a mucro, pale to reddish brown. *Inflorescence* very contracted, panicle-like or subcapitate and appearing head-like, straight to somewhat flexuous, with 2–6 nodes, 0.5–1.7 cm long, 6–16 mm wide, not interrupted; bracts leaf-like, greatly exceeding the spikelet clusters in length, sheaths in the lower part of the inflorescence open, not or sometimes enveloping the higher bracts, gradually reducing along the inflorescence and often mostly hidden among the spikelets, basal bract spreading to sub-erect, similar to the leaves, much longer than the inflorescence, to 65 mm long; branches erect to spreading, with 2–5 spikelets in a terminal cluster, spikelet(s) on short, terete, glabrous peduncles 0.2–1.4 mm long, arising in each bract axil; basal branchlet 4.5–6.6. mm long (including spikelets); spikelet prophyll present, sheath 0.9–1.5 mm long, brown, partially enclosing the spikelet, with a slender lamina 0.2–1.6 mm long, brown. *Spikelets* pale to dark brown or chestnut, narrow-ovate, 4.7–8 mm long, 1.2–3.2 mm wide, terete, with 5–9 glumes, only topmost 1 or 3 fertile, the lower 2 flowers when present male fertile, the upper flower bisexual, fertile, no reduced glume above the florets; glumes spirodistichous, basal glume 2.6–4.2 mm long, fertile glumes 3.8–6.2 mm long, 0.9–1.6 mm wide, membranous, pale to dark brown or chestnut, lamina puberulent or glabrous, keel and margins scaberulous, ciliate or denticulate, acute or attenuate, often sparsely scabrous on the keel, usually ciliate on the margins, lamina glabrous, ovate-lanceolate, acute to acuminate or obtuse, with a mucro 0.3–1.2 mm long, keel distinct; rachilla compact and not sinuous in fruiting spikelets. *Perianth segments* 6, whitish, minute, ± linear, flat to terete, margins with dense to scattered, white, short, antrorse, ciliate or ciliate-plumose hairs, persistent on the nutlet. *Stamens* 3; anther connective 2.0–6.2 mm long, linear to subulate; anthers yellow, 1.8–3.1 mm long, twisted when dry, with a glabrous apical appendage 0.5–0.8 mm long. *Style* trifid, base 1.4–3.5 mm long, glabrous, slender throughout, branches 1.3–2.9 mm long, hispidulous. *Nutlet* stipitate, stipe 0.3–0.5 mm long, somewhat constricted, obovoid to obpyriform, obscurely trigonous, dull, brown to dark brown, reddish brown or grey, 1.4–2.3 mm long including the stipe and style base, 1.0–1.4 mm diam., faces irregularly reticulate to rugulose or tuberculate at 40× magnification, shortly hispidulous to scabrous or tuberculate at the apex, otherwise glabrous; epidermal cells usually square–hexagonal, inconspicuous, with three fine white ribs, style base not enlarged, thin, sometimes part of the base persistent, cylindrical; embryo Schoenus-type. Photosynthetic pathway inferred from anatomy to be C_3. 1C = 0.26 pg for *C. turbinata* (*K.L. Wilson 10781*; Bureš *et al.* 2013).

Diagnostic characters: This genus is characterised by the combination of pseudobulbous bases, leaves with a well-developed lamina; a capitate or turbinate inflorescence subtended by several involucral bracts that greatly exceed the spikelets; the inflorescence branches supporting 1–3 spikelets each, the branches very short and hidden below the spikelets; a non-flexuous, straight rachilla with very short internodes; and flattened to terete, hairy perianth segments.

Distribution: Three species endemic to the southern Australia, one eastern and two western.

Etymology: A combination of the Greek words *chaete* (bristle) and *spora* (a seed), not defined by Brown (1810), but inferred to be referring to the nutlet surrounded by bristles.

Notes: A lectotype for the genus was chosen by Barrett *et al.* (2020a) while revising the genus, allowing the name to be separated from *Schoenus* and used for three species endemic to southern Australia. Descriptions and illustrations of the three species recognised are presented in Barrett *et al.* (2020a). The generic description above has been expanded from Barrett *et al.* (2020a) to be comparable to the description of *Tricostularia* presented below.

Key to species of *Chaetospora* (from Barrett *et al*. 2020a)

1. Inflorescence ± obovoid; leaf sheath 4–7 cm long (SE Australia)..... ***C. turbinata***

1: Inflorescence ± globose to depressed globose; leaf sheath 2–4 cm long (SW Australia) 2

2. Flower head usually black (sometimes dark brown); spikelets 1-flowered; perianth segments flat, ciliate, 1.5–2 mm long (about as long as the nutlet) ..... ***C. curvifolia***

2: Flower head rather pale brown; spikelets 3-flowered; perianth segments compressed to terete, 0.2–0.4 mm long (much shorter than the nutlet) ..... ***C. subbulbosa***

Morelotia Gaudich., *Voy. Uranie* 4(10): 416 (1829).

Type species: *Morelotia gahniiformis* Gaudich.

Tetrariopsis C.B.Clarke, *Bull. Misc. Inf., Kew – Add. Ser.* 8: 45 (1908), *syn. nov*.

Type species: *Tetrariopsis octandra* (Nees) C.B.Clarke.

[*Tetrariopsis* C.B.Clarke in L.Diels & E.Pritzel, *Bot. Jahrb. Syst., Pflanzenges. Pflanzengeog.* 35(1): 81 (1904), *nom. inval., nom. nud.*]

Perennial tufted herbs, 0.7–1.2 m high; plants clonal, 0.2–0.8 m across; rhizome thick, woody, short, branched, 5–15 mm diam., pseudobulbous or not; old leaf sheaths covering the rhizome, breaking apart into fibres with age or not, dark brown to blackish brown; roots sand-binding or not. *Culms* stout, erect, with 0, 1 3 or 4 leafy nodes, trigonous or ± terete, 1.0–5.5 mm diam., multi-striate, glabrous or rugulose. *Caudex* absent. *Leaves* mostly basal, numerous, and with 0, 1 3 or 4 cauline; phyllotaxy loosely spirotristichous, sheath glabrous or sometimes pubescent (then glabrescent), tight around culm, 8–60 mm long, 1.2–6 mm wide, ± equal in width to or broader than the leaf lamina, pale brown to dark brown to blackish brown, upper margin usually with fine, blunt scabrous projections, ligule absent; *pseudopetiole* present or not obvious; basal leaves 12–62 cm long, 2–8 mm wide, lamina ± linear, sometimes twisted or curved, finely multi-striate, glabrous or midrib scabrous, dark green, often slightly paler below, margins usually finely bluntly scabrous, sometimes revolute or involute, apex long-attenuate. *Inflorescence* open or dense, panicle-like, narrow, linear to lanceolate, 5–35 cm long, 5–35 mm wide, axis green, not glaucous; with 3–8 nodes; bracts leaf-like, becoming progressively smaller up the culm, ± equal to greatly exceeding the spikelet clusters, basal bract shorter than to exceeding inflorescence; branches erect, basal branch 2–7 cm long, with 2–20 clustered spikelets on peduncles 0.5–5 mm long, arising in each bract axil; spikelet prophyll present, sheath 1.2–4.5 mm long, brown, with 3 distinct veins, partially enclosing the spikelet, with a slender lamina 0.2–8.5 mm long, brown to green. *Spikelets* chestnut to brown, lanceolate to ovate, 6.5–15 mm long, not compressed, with 5–8, rarely 9, glumes, usually 1 or 2 fertile florets, sometimes 3, upper glume with a sterile male flower, second upper glume bisexual fertile, lower glumes empty, or rarely the third upper glume with a bisexual sterile or male-fertile flower, glumes spirodistichous, basal glume 2.5–7.8 mm long, fertile glumes 4.5–11.5 mm long, 1.6–3.5 mm wide, glabrous, scabrous or pubescent, especially on keel and towards the apex, elliptic-lanceolate, acute to acuminate, weakly keeled, with a mucro 0.4–3.0 mm long; rachilla mostly compact, but shortly sinuous around nutlet in fruiting spikelets in some species. *Perianth segments* absent or sometimes 2 or 6 segments present, 0.4–1.6 mm long, filiform, glabrous. *Stamens* usually 3, 6 or 8, rarely also 4 or 9; anther connective 4.3–9.6 mm long, linear; anthers yellow or pale yellow, 3.1–6.5 mm long, linear-oblong, base auriculate, with a glabrous or scaberulous apical appendage 0.5–2.0 mm long. *Style* usually 3-branched (but 3–5 in *M. octandra*), base 3–7.3 mm long, glabrous or finely scabrous, thin above, thin or dilated below, branches 2.5–10 mm long. *Nutlet* straw-coloured, pale brown, brown or black, sessile (or shortly stipitate in *M. microcarpa*), angular globose, strongly 3(–5)-ribbed, 2.1–5.4 mm long including the style base, 0.8–2.3 mm diam., epidermal cells square, oblong, semi-circular or hexagonal, but inconspicuous; apex sometimes with a very distinct persistent style base, depressed-ovoid, pyramidal or shortly conical, somewhat constricted at the base, scabrous-pubescent, 0.5–2.0 mm long; embryo Schoenus-type. Photosynthetic pathway inferred from anatomy to be C_3.

Diagnostic characters: Culms with 0, 1, 3 or 4 nodes below the inflorescence; caudex absent; leaf lamina well-developed, 12–62 cm long, 2–8 mm wide; involucral bracts leaf-like; inflorescence open, elongate or dense, panicle-like, 5–35 cm long, branches erect to spreading; rachilla curved around nutlet or not; perianth segments 0, 2 or 6, 0–1.5 mm long; nutlets ± sessile (or shortly stipitate in *M. microcarpa*).

Distribution: Three species endemic to the Pacific (one each in Hawai'i, French Polynesia and New Zealand), and three endemic to southern Western Australia.

Etymology: Named for French pharmacist Simon Morelot (1751–1809), author of several books on pharmacy and natural sciences.

Notes: While Clarke (1904) provided a direct reference to a published species description (Bentham 1878), this is not sufficient to validate his proposed generic name *Tetrariopsis* and therefore the new combination *Tetrariopsis octandra* is also invalid in that publication (Turland *et al.* 2018; Art. 38.11). Both the genus and new combination were subsequently validly published by Clarke (1908).

The inclusion of *Machaerina involuta*, *Tetraria australiensis*, *T. microcarpa* and *Tetrariopsis octandra* in *Morelotia* significantly increases the range of morphological diversity in the genus relative to previous treatments.

Historically, *Morelotia* has commonly been included in *Gahnia*. Spikelet prophylls are present in *Morelotia* (absent in *Gahnia*), described as 'scale-leaves' by Benl (1940a,b; 1950) and 'prophylls' by Blake (1969). These are found at the base of all ramifications of the inflorescence (including below each spikelet). Bruhl (1992, 1995) differentiated these as 'prophylls' and 'spikelet prophylls', and we follow this here. Ligules are absent in *Morelotia*, and the rachilla is elongated and curved around the nutlet (Blake 1969). Species of *Gahnia* have a leaf ligule, lack spikelet prophylls, and have a compact rachilla (Blake 1969).

Excellent diagrams of the floral structure in *Morelotia affinis* and *M. gaudichaudii* are provided by Kern (1962, fig. 1). Kern (1962) considered *Morelotia affinis and M. gaudichaudii* to belong in *Machaerina* based on the trigonous culms, revolute leaves, distichous glumes, presence of an imperfect second flower and greatly thickened style-base. This may have influenced St John's decision to describe his new species as *Machaerina involuta* (St John 1984), but no notes to this effect have been found. Blake (1969) pointed out that *Machaerina* differs significantly from *Morelotia* as *Machaerina* lacks trigonous culms, dorsiventral, revolute leaves, and distichous, deciduous glumes, and has a compact rachilla.

Key to species of *Morelotia*

1. Culms rugulose-asperulous on faces, scabrid on angles; inflorescence subspiciform, with 12–20 spikelets per branchlet; spikelets 3.5–4 mm long, with 3 fertile flowers; basal glume 1.2–2.2 mm long, fertile glumes 2.6–3.4 mm long, 0.7–0.9 mm wide; anthers 0.8–0.9 mm long, connective 1.8–2.5 mm long; style 3.1–3.8 mm long; nutlets 1.4–1.7 mm long (SW Australia)..... ***M. microcarpa***

1: Culms glabrous; inflorescence open or dense, panicle-like, with 2–15 spikelets per branchlet; spikelets 6.5–15 mm long, with 1 or 2 fertile flowers; basal glume 2.5–7.8 mm long, fertile glumes 4.5–11.5 mm long, 1.6–3.4 mm wide; anthers 3.1–6.5 mm long, connective 4.3–9.6 mm long; style 7–15 mm long; nutlets 2.1–5.4 mm long..... 2

2. Ramets at least somewhat pseudobulbous; roots sand-binding; leaf sheaths clasping the culms; leaf lamina flat, channelled or revolute; basal glume 5.0–7.8 mm long; upper flower bisexual fertile; stamens 6 or 8; style 5–7.3 mm long; nutlets 4.5–5.4 mm long, apex scabrous or hispidulous..... 3

2: Ramets not pseudobulbous; roots not sand-binding; leaf sheaths loose on the culms; leaf lamina flat, becoming involute and often appearing terete with age; basal glume 2.5–4.1 mm long; upper flower infertile; stamens 3; style 3–5.1 mm long; nutlets 2.1–3 mm long, apex glabrous 4

3. Culms with 3 or 4 nodes below the inflorescence; leaf sheath pubescent (at least when young); leaf lamina 12–18 mm long; spikelets 8–10 mm long; 5 glabrous glumes; rachilla compact; and usually 6 anthers (SW Australia)..... ***M. australiensis***

3: Culms with 0 or 1 nodes below the inflorescence; leaf sheath glabrous; leaf lamina 15–60 cm long; spikelets 10–15 mm long; 7–9 scabrous to pubescent glumes; rachilla curved around the nutlet; and usually 8 anthers (SW Australia) ..... ***M. octandra***

4. Culms always with a single node below the inflorescence; 1.3–1.7 mm broad; basal leaves 2.5–4 mm wide, involute, appearing 1–1.3 mm wide, margins very finely scabrous, usually recurved when dry; inflorescence branches 20–25 mm long, with (1)2 or 3 clustered spikelets; perianth segments present, filiform, 0.4–1.1 mm long; nutlet mostly stramineous but apex brown (Rapa Iti, French Polynesia) ..... ***M. involuta***

4: Culms variously with 0–4 nodes below the inflorescence; 1.5–3.8 mm broad; basal leaves 2–8 mm wide, involute, appearing 1.5–2.5 mm wide, margins harshly scabrous, usually strongly revolute when dry; inflorescence branches 20–70 mm long, with 2–15 clustered spikelets; perianth segments absent; nutlet lustrous red-brown to black, apex black..... 5

5. Leaves rapidly and completely revolute; leaf sheath 35–60 mm long; leaf lamina midrib hairy; spikelets reddish brown; basal glume 2.4–2.8 mm long; fertile glumes puberulent; nutlet apex subconical, epidermal cells semi-circular to hexagonal (New Zealand) ..... ***M. affinis***

5: Leaves slowly and usually incompletely revolute; leaf sheath 25–39 mm long; leaf lamina midrib glabrous; spikelets brown; basal glume 3.8–4.1 mm long; fertile glumes hispidulous; nutlet apex obtuse-apiculate, epidermal cells oblong to square–hexagonal (Hawaii) ..... ***M. gahniiformis***

Morelotia affinis (Brongn.) S.T.Blake, *Contr. Queensland Herb.* 8: 38 (1969). *Lampocarya affinis* Brongn. in L.I.Duperrey, *Voy. Monde, Phan.* (part 11); 166–167, t. 29, figs 1–4 (1833). *Schoenus arenarius* Banks & Sol. ex Hook.f., *Fl. Nov. Zel.* 1: 277 (1853), *nom. illeg.*, *in syn.*, *non* Schrad. (1832). *Gahnia affinis* (Brongn.) Steud., *Syn. Pl. Glumac.* 2: 164 (1855). *Gahnia arenaria* Hook.f., *Handb. N. Zeal. Fl.* 1: 306 (1864), *nom. illeg. Mariscus affinis* (Brongn.) Kuntze, *Revis. Gen. Pl.* 2: 755 (1891). *Machaerina affinis* (Brongn.) J.Kern, *Acta Bot. Neerl.* 11: 223 (1962).

Type citation: 'Nouvelle-Zélande.'

Type: New Zealand: Voy. Astrolabe, [1827], *J.S.C.D. d'Urville s.n.* (lectotype (here designated): P 00601899* [excluding fruit of *M. gaudichaudii* in packet]; probable isolecto: P 01869436*).

Morelotia gahniiformis var. *minor* A.Rich., *Fl. Nuov. Zel.* 115 (1832).

Type citation: 'Crescit in Novae-Zeelandiae loco dicto *baie des Iles.* (v. s. s.)'

Type: New Zealand: Baie des Iles [Bay of Islands], [Mar. 1827] Voy. Astrolabe, [*J.S.C.D. d'Urville & R-P. Lesson*] *No. 39* (lectotype (here designated): P 01869439*).

Residual syntypes: New Zealand: Baie des Iles [Bay of Islands], Voy. Astrolabe, [*J.S.C.D. d'Urville & R-P. Lesson s.n.*] P 01869438*, P 01869440*; [*J.S.C.D. d'Urville & R-P. Lesson No. 28*] P 01869441*).

Cladium quadrangulare Nees, *Linnaea* 9: 301 (1834), *nom. inval., nom. nud.*

Illustrations: Illustration on sheet: P 01869438. Brongniart in Duperrey (1833, t. 29, figs 1–4; reproduced by St John 1958 as fig. 1, No. 1–4); Kern (1962, fig. 1: 8–11).

Perennial tufted *herb*, 0.2–0.7 m high; plants presumably clonal, 0.4–1 m across; rhizome thick, woody, short, branched, 5–10 mm diam., pseudobulbous; old leaf sheaths covering the rhizome, breaking apart into fibres and the leaf base becoming twisted with age, cream to pale brown; roots not sand-binding. *Culms* stout, erect, with 0–2(–4) leafy nodes, trigonous, 1.9–3.5 mm broad, smooth, glabrous, base not enlarged. *Leaves* mostly basal, numerous, and 0–2(–4) cauline; phyllotaxy loosely spirotristichous, sheath striate, margin finely scabrous, otherwise glabrous, open, 35–60 mm long, 4–6 mm wide, broader than the leaf lamina, cream, upper margin membranous, ligule absent; basal leaves 20–62 cm long, 4–8 mm wide, but becoming involute and appearing filiform and 1.5–2.1 mm wide with age, lamina dorsiventral, ± linear, curved, finely multi-striate, scabrid below, especially on midrib, green to yellow-green (rarely dark green), slightly paler below, margins harshly scabrous, strongly revolute when dry, apex gradually attenuate and curled when dry; cauline leaf lamina 15–20 cm long. *Inflorescence* dense, panicle-like, narrow, linear, 5–30 cm long, 15–35 mm wide, with 5–8 fertile nodes; axis green; bracts leaf-like, rigid, scabrid, with pale brown sheaths 10–35 mm long, becoming progressively smaller up the culm, greatly exceeding the spikelet clusters, basal bract ± equal to inflorescence; branches 20–70 mm long, erect, with 3–15 clustered spikelets on peduncles 0.5–1 mm long, arising in each bract axil; spikelet prophyll present, sheath indistinct, lamina 1.4–1.6 mm long, brown, with 1 distinct vein. *Spikelets* reddish brown, narrow-lanceolate to ovate-lanceolate, 6.5–10 mm long, 1.4–2.2 mm diam., ascending, not compressed, with usually 7 glumes, the topmost infertile, subtended by a minute membranous glume, upper 2 larger glumes each subtending a flower, enclosed by the wing of the next glume, lower flower bisexual, upper functionally male, lower glumes empty, glumes distichous (basal glumes somewhat twisting with age so can appear spirodistichous), somewhat compressed, coriaceous, lower glumes caducous, basal glume 2.4–2.8 mm long, fertile glumes 4.5–9 mm long, 1.8–3.4 mm wide, minutely puberulous, lanceolate, acuminate to acute, keeled, the keel and margins finely scabrid, sometimes with a mucro to 0.4 mm long; rachilla compact, but the uppermost internode elongated and curved in fruiting spikelets. *Perianth segments* absent. *Stamens* 3; anther connective 6.3–8.8 mm long, elongating further after anthesis, linear, persistent at base of nutlet, distal portion held within the convolute apex of subtending glume, so mature nutlets pendent on the inflorescence post-release; anthers yellow, 3.6–4.2 mm long, linear-oblong, base auriculate, with a glabrous apical appendage up to 1.4 mm long. *Style* 3-fid, base 3.9–4.2 mm long, hispidulous, thin throughout, branches 3.1–3.7 mm long, hispidulous-papillose. *Nutlet* sessile, elliptic-obloid, subterete but somewhat trigonous, with 3 longitudinal ribs, lustrous red-brown to black, apex black and subconical, smooth, 2.5–3.0 mm long including the style base, *c.* 1.5 mm diam., mesocarp crustaceous, epidermal cells semi-circular–hexagonal, conspicuous; style base thickened, somewhat corky, persistent, very distinct in the immature fruit, less distinct at maturity, glabrous, *c.* 0.9 mm long; embryo not examined. Photosynthetic pathway inferred from anatomy to be C_3 (*Bagnall s.n.*, CHR 56270; Bruhl & Wilson 2007). $2n = 46$ (de Lange *et al.* 2004). (Figure 6).

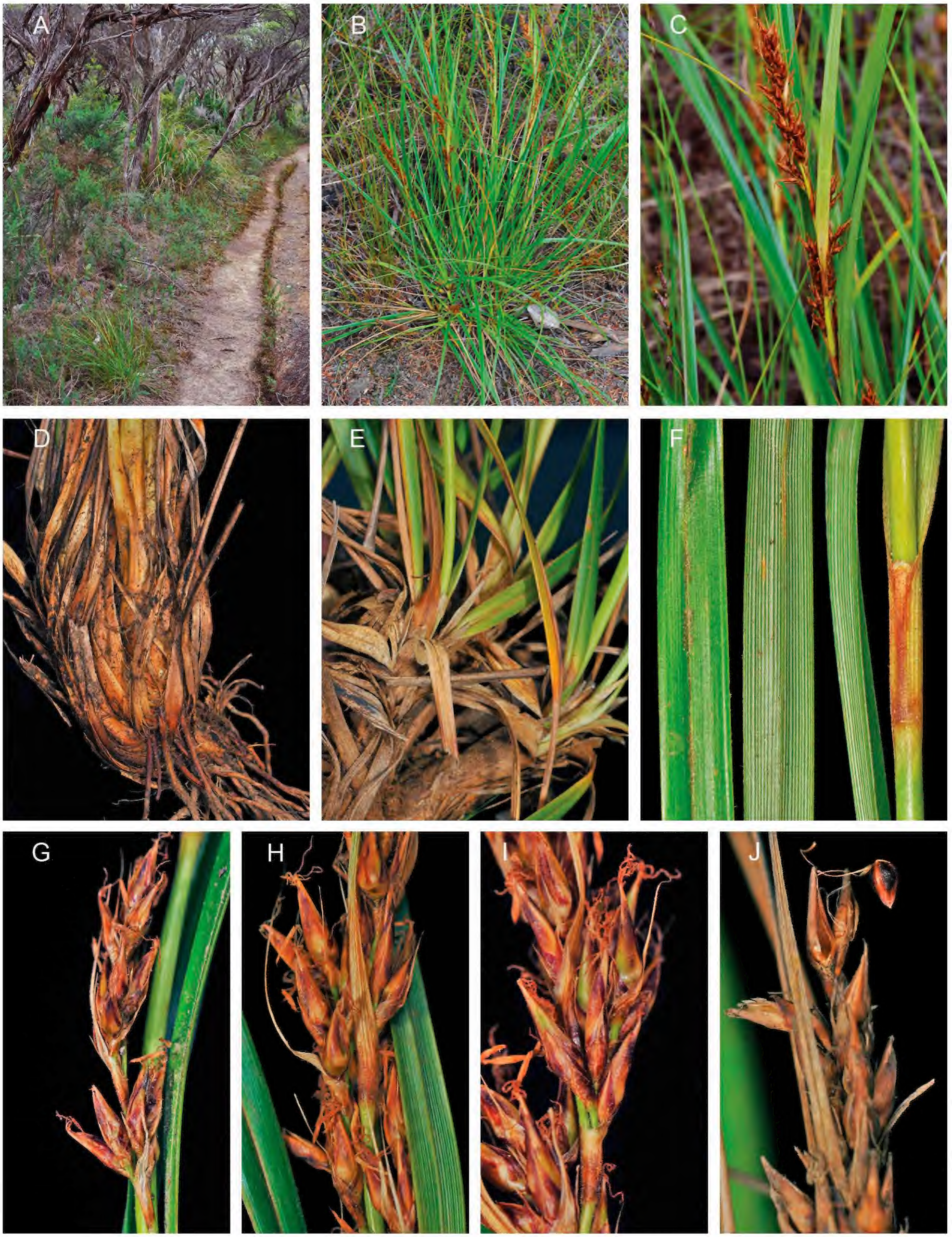

Fig. 6. *Morelotia affinis*. Whatipu, North Island, New Zealand. A. Habitat. B. Habit. C. Inflorescence. D. Plant base and roots. E. Plant base and leaf rosette. F. Leaf above (left), leaf below (2 central), cauline leaf sheath (right). G, H. Spikelets with old stamens. I. Spikelets with old styles. J. Spikelets with mature nutlet held by persistent anther filaments. Vouchers, A–D, F, G, I from *J.J. Bruhl 2923* (NE); E, H, J from *J.J. Bruhl 2924* (NE). Photos by J.J. Bruhl.

Diagnostic characters: Differs from *M. gahniiformis* in the leaves being more rapidly and completely revolute; leaf sheath 35–60 mm long (*vs* 25–39); leaf lamina midrib hairy (*vs* glabrous); spikelets reddish brown (*vs* brown); basal glume 2.4–2.8 mm long (*vs* 3.8–4.1); fertile glumes puberulent (*vs* hispidulous); the nutlet apex subconical (*vs* obtuse-apiculate), epidermal cells semi-circular–hexagonal (*vs* oblong–square–hexagonal).

Distribution: Endemic to New Zealand, widespread on the North Island, but rare on the South Island, with records near Nelson and Christchurch (Edgar 1970).

Habitat: Grows in a wide range of coastal to montane habitats with a variety of soils and geologies, but usually on steep clay banks, cliff faces and hillsides, and known to readily colonise steep rock faces and boulder falls. Recorded in gumland scrub, Kauri forest, Manuka forest and shrublands in association with *Acaena pallida*, *Apodasmia similis*, *Astelia banksii*, *A. trinervia*, *Carex appressa*, *C. geminata*, *C. fascicularis*, *C. flagellifera*, *C. forsteri*, *C. healyi*, *C. minor*, *C. pumila*, *C. punctata*, *C. uncinata*, *Celmisia major*, *Coprosma baueri*, *C. microcarpa*, *Cordyline* spp., *Cyperus ustulatus*, *Eleocharis neozealandica*, *Epacris pauciflora*, *Euphrasia cuneata*, *Ficinia spiralis*, *Gahnia pauciflora*, *G. setifolia*, *Geranium homeanum*, *Gleichenia microphylla*, *Isolepis cernua*, *Knightia excelsa*, *Lepidosperma australe*, *Leptospermum scoparium*, *Leucopogon fasciculatus*, *L. fraseri*, *Lycopodium* spp., *Machaerina rubiginosa*, *Meterosideros exselsa*, *Myrsine australis*, *Ozothamnus leptophyllus*, *Phyllocladus* spp., *Pittosporum eugenioides*, *Pomaderris rugosa*, *Schoenus tendo* and *Veronica obtusata*.

Phenology: Flowers recorded for October–December. Fruiting recorded for (October–)November–April, but old inflorescences are persistent.

Selected specimens examined: NEW ZEALAND: [island not specified]: 1854, *W. Hooker s.n.* (P*); 'New South Wales' [New Zealand], 1838–1842, *Wilkes Expedition* (US*). NORTH ISLAND: Mahina Bay, 26 Aug. 1941, *G. Bagnell s.n.* (CHR 56270, *n.v.*, NSW); near Tolaga, Opuragi, Oouhuragi, 1769, *J. Banks & D.C. Solander s.n.* (AK 109793*, BM 000991155*, US 02234605*, WELT SP063907*); Waitakere Ranges, Kaitarakihi Park, site of Nov 1983 burn, 6 Nov. 1987, *R.E. Beaver s.n.* (AK 156546*); Waitakere Ranges Regional Parkland, 1.4 km N of Whatipu Lodge, along walking track, 5 Dec. 2010, *J.J. Bruhl 2923* (NE); Motukino (Fanal) Island, W side. Taranga Ecological District, 21 Sept. 1994, *E.K. Cameron & P.J. de Lange 7788* (AK, *n.v.*, HO); Parahaki, Oct. 1898, *H. Carse s.n.* (AK 214665*); near Tirau (Oxford), Oct. 1896, *T.F. Cheeseman s.n.* (AK 214664*); Mangorewa River, Tauranga County, 15 Oct. 1965, *R.C. Cooper s.n.* (AK, *n.v.*, NSW); North Auckland, Kaukapakapa Gumlands, 28 Jan 1961, *A.E. Esler s.n.* (AK 363112*); Auckland, 1875, *M. Filhol 860* (P*); hills south of Piha, West Coast, west of Auckland, 4 Feb. 1949, *F.R. Fosberg 30221* (US*); 3.3 km S of Ahipara, Ahipara Gumfields Historic Reserve, 17 July 1990, 30 Apr. 1990, *J. Fox s.n.* (AK 374668*, WELT, *n.v.*); Craigavon Park, Auckland, 3 Mar. 1974, *R.O. Gardner 864* (AK, *n.v.*, CBG); Waitakere Ranges, 1942, *E.T. Giles s.n.* (NE 21620); [Lake] Taupo, 1873, *Gohenacker s.n.* (P*); Te Paki, North Cape Peninsula, Surville Cliffs, 19 Oct. 2009, *P.J. de Lange 8023* (AK, *n.v.*, CHR, *n.v.*, NSW, WELT, *n.v.*); Days Bay, Eastbourne, Wellington, 4 Oct. 1948, *R. Mason s.n.* (CHR, *n.v.*, NSW); Auckland, Sept. 1929, *A. Meebold 5346* (US*); Shag Track, Little Barrier Island, 7 Mar. 1962, *R. Melville & W.M. Hamilton 6614* (K, NSW); road between Paengoroa and Lake Rotaiti, 27 Oct. 1964, *C.C. Ogle s.n.* (WELT SP106926*); North Cape Peninsula, 25 Nov. 1916, *R.B. Oliver s.n.* (WELT SP010160*); Auckland, early Nov. 1911, *D. Petrie s.n.* (AK, *n.v.*, NSW); Auckland, 1850–1860, *A. Sinclair s.n.* (NSW); Wellington, Jan. 1909, *H.H. Travers s.n.* [*?221*] (P*); Kawakawa [Bay], *J.S.C.D. d'Urville 333* (P, 3 sheets*); Koangata, [rec. 1824], *J.S.C.D. d'Urville s.n.* (P*); near Babylon, south of Kaihu, 8 Apr. 1947, *E.H. Walker 5268* (US*). SOUTH ISLAND: Akaroa, *St. Croix de Belligny s.n.* (P*).

Conservation: Relatively widespread on the North Island of New Zealand, occurring in numerous nature reserves, and listed as Not Threatened (de Lange *et al.* 2018). IUCN: Least Concern.

Etymology: From the Latin *affinis* (near), possibly referring to the similarities of this species to *Lampocarya gaudichaudii* Brongn. (=*Morelotia gahniiformis*), but the original intent is not known.

Notes: The lectotype of *Lampocarya affinis* is chosen as it is the only sheet at P bearing a label '*Lampocarya affinis* Brongn. nov. spec.' As noted by St John (1958), there are several fruit of *M. gahniiformis* in a packet on the lectotype sheet (but excluded above), presumably those used for the illustration in t. XXIX, fig. 5 (Brongniart in Duperrey 1833). Fruit were evidently removed previously from both sheets of both species for illustration, and presumably returned to the wrong sheet by mistake as the same error has occurred on a type sheet of *M. gahniiformis*. These fruit are therefore specifically excluded from the type statement above.

Both P 01869439 and P 01869441 are from Richard's herbarium, and are suitable for selection as lectotype of *Morelotia gahniiformis* Gaudich. var. *minor* A.Rich. Neither sheet has been annotated with the varietal name. P 01869439 is selected as there is more material on the sheet. Richard (1832) provided extensive notes on the differences between the Hawaiian and New Zealand *Morelotia* specimens, but conservatively only separated them at varietal level.

The invalid name *Cladium quadrangulare* Nees was published without any description and can only be assigned based on specimen annotations. The sheet P 01869420 is annotated with this name, and belongs to *G. affinis*, not *M. gahniiformis* where it is traditionally included. Heller (1896) noted that Nees (1834) separated

this taxon from *M. gahniiformis*, supporting the idea that it more likely applies to the taxon now recognised as *G. affinis*.

Seed is noted to be difficult to germinate and probably exhibits physical dormancy (New Zealand Plant Conservation Network 2020).

Moar and Wilmshurst (2003) report that the pollen grains of *M. affinis* are similar to those of *Gahnia procera* J.R.Forst. & G.Forst. and *G. xanthocarpa* Hook.f. (*Gahnia*-type).

Morelotia australiensis (C.B.Clarke) R.L.Barrett & K.L.Wilson, ***comb. nov.***

Basionym: *Tetraria australiensis* C.B.Clarke in L.Diels & E.Pritzel, *Bot. Jahrb. Syst., Pflanzenges. Pflanzengeog.* 35(1): 80–81, fig. 5g–q (1904).

Type citation: 'Hab. in distr. Darling pr. Serpentine Riv. in silvis apertis arenosis subhumosis flor. m. Decembr. (E. Pritzel Plant. Austr. occ. 138; D. 1872).'

Type: Serpentine River, Western Australia, 1900, *F.L.E. Diels 1872* (lectotype (here designated): K 000960103 (ex B); isolecto: PERTH 01049585 (fragment)).

Residual syntype: Murray District, Western Australia, Dec. 1900, *E. Pritzel* [*Plant. Austr. Occid. 138*] (syn: BM 000798892, E 00688600, G 00195291, G 00195292, K 000960104, L 0042803, NSW 687847).

Illustrations: Clarke in Diels & Pritzel (1904: 82, fig. 5g–q); Wheeler & Graham (2002: fig., p. 297); Brown *et al.* (2008: pl., p. 150).

Perennial (short-lived) tufted herb, 0.3–1.3 m high; plants clonal, 0.1–0.6 m across; rhizome short, thick, woody, 8–15 mm diam., not pseudobulbous; old leaf sheaths covering the rhizome, not breaking apart into fibres with age, dark brown to blackish brown; roots sand-binding. *Culms* stout, erect, with 3 or 4 distant, leafy nodes, ± terete, 2.0–5.5 mm diam., multi-striate, glabrous, base not or slightly enlarged. *Leaves* mostly basal, numerous, and 3 or 4 cauline, reducing in size up the culm, ultimately bract-like; phyllotaxy loosely spirotristichous, sheath pubescent (?glabrescent), tight around culm, 20–45 mm long, 3–6 mm wide, ±equal width to the leaf lamina, dark brown to blackish brown, upper margin glabrous, ligule absent; basal leaves 12–18 cm long, 2–6 mm wide, lamina ±linear, channelled to ± flat, finely multi-striate, pubescent when young, green to blue-green, paler below, margins sparsely scabrous, sometimes recurved, apex long-attenuate. *Inflorescence* open, panicle-like, narrow, ± linear, 15–27 cm long, 10–20 mm wide, axis blue-green, yellow-green or pinkish brown, slightly glaucous; bracts leaf-like, shorter than to slightly exceeding the spikelet clusters, basal bract much shorter than inflorescence; branches erect, with 3–10 densely clustered spikelets on short peduncles 1–2 mm long, arising in each bract axil; spikelet prophyll subtending each spikelet glume-like, sheath 3.7–4.1 mm long, pale brown, with 1 indistinct vein, partially enclosing the spikelet, without a lamina. *Spikelets* pale brown (apex of glumes reddish when young), very narrow-ovoid, 8–10 mm long, laterally compressed, with usually 5 glumes, glabrous but cell surface raised so appears very finely papillose at 20× magnification, only topmost 2 fertile, the lower flower bisexual but often reduced and infertile, the upper flower bisexual, fertile, lower glume 6–7 mm long, fertile glumes 7–9 mm long, 1.6–2.1 mm wide, glabrous, acute to obtuse with a mucro to 1.5 mm long; rachilla compact and not sinuous in fruiting spikelets. *Perianth segments* absent. *Stamens* (3)6 in upper flower, 6 in lower flower; anther connective 5–7 mm long, linear; anthers yellow, 5.5–6.5 mm long, with a scaberulous apical appendage up to 1 mm long. *Style* trifid, base 5–7 mm long, not dilated, glabrous, branches 2.5–3.0 mm long. *Nutlet* sessile, ovoid to ellipsoid, 4.9–5.4 mm long, 2.0–2.3 mm diam., smooth, epidermal cells square–hexagonal, inconspicuous, with 4 or 5 distinctly raised white ribs that broaden and fuse with the apex, apex with a very distinct persistent style base, broadly subconical to pyramidal, somewhat constricted at the base, to 1.4 mm long, finely hispidulous; embryo not examined. Photosynthetic pathway not examined. 1C = 0.49 pg (*BGPA 20100981*; Bureš *et al.* 2013). (Figure 7).

Diagnostic characters: Differs from *Morelotia octandra* in its 3 or 4 (*vs* 0 or 1) nodes below the inflorescence; pubescent (at least when young) (*vs* glabrous) leaf sheath; leaf lamina 12–18 (*vs* 15–60) cm long; spikelets 8–10 (*vs* 10–15) mm long; 5 glabrous (*vs* 7–9 scabrous to pubescent) glumes; rachilla compact (*vs* curved around the nutlet); and usually 6 (*vs* usually 8) anthers.

Distribution: Apparently endemic to the greater Perth region, occurring on the eastern side of the Swan Coastal Plain, from Busselton, Mundijong and Waroona, north to Serpentine. Historical populations near the Perth suburbs of Armadale and Canning are apparently now extinct.

Habitat: Usually in winter-wet swampy depressions, drainage lines or sandy rises adjacent swamps, growing in grey sand over clay or yellow and sandy or clayey lateritic soils. In open *Corymbia calophylla* or *Eucalyptus marginata* woodland over low shrubs, herbs and sedges in association with *Anigozanthos*

humilis, *Banksia attenuata*, *B. aurantia*, *B. menziesii*, *Conostylis setigera*, *Cyathochaeta avenacea*, *Eremaea pauciflora*, *Haemodorum* sp., *Hakea ruscifolia*, *H. cyclocarpa*, *Isolepis marginata*, *Kingia australis*, *Lechenaultia biloba*, *Lepidosperma carphoides*, *Melaleuca* sp., *Mesomelaena tetragona*, *Pericalymma ellipticum*, *Schoenus asperocarpus*, *S. lanatus*, *S. rodwayanus*, *S. subbarbatus*, *Morelotia octandra* and *Xanthorrhoea preissii*.

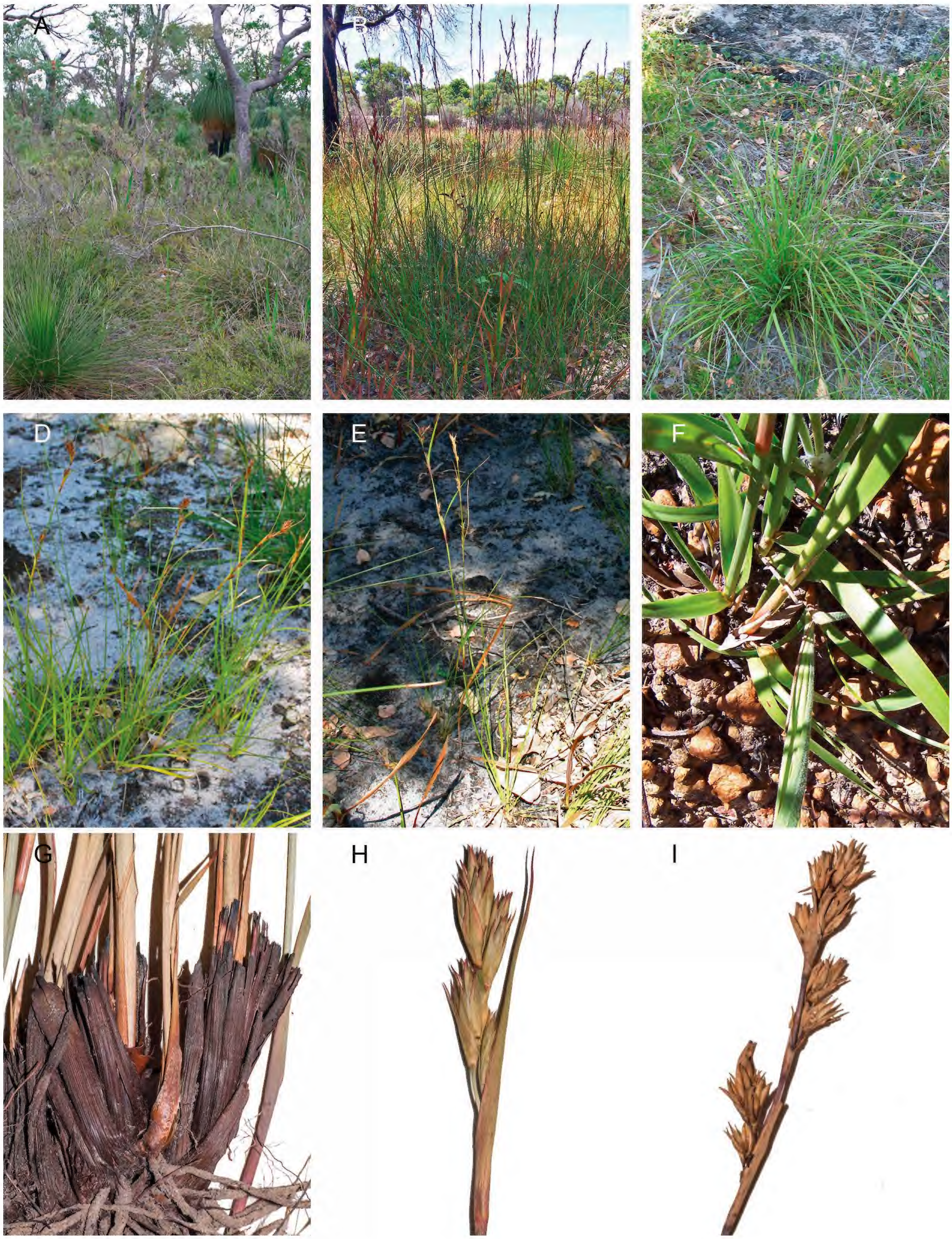

Fig. 7. *Morelotia australiensis*. A. Habitat. B. Plants in habitat. C. Plant with old inflorescences. D, E. Flowering plants. F. Leaf and culm bases. G. Plant base with new growth after fire. H, I. Inflorescence. A–E, G–I from Watkins Reserve. F from North Dandalup. G–I from *K.L. Wilson 9310* (NSW). Photos A, B, D–F by M. Okely; C. by V. English; G–I by R.L. Barrett.

Phenology: Flowers recorded for October–February, usually one year post-fire. Fruit recorded for January, February, June and October.

Selected specimens examined: WESTERN AUSTRALIA: [localities withheld] Dec. 1898, *R. Helms s.n.* (NSW 75057); Feb. 2010, *M. Hoskins & F. Felton MH 30* (PERTH); Nov. 1995, *B.J. Keighery 2270* (NSW, PERTH); Feb. 1996, *B.J. Keighery 2365a* (PERTH); Feb. 1996, *B.J. Keighery 2384* (PERTH); Feb. 1996, *B.J. Keighery 2385* (NSW, PERTH); Jan. 1993, *G.J. Keighery 12792* (CANB, MEL, PERTH); Jan. 1996, *G.J. Keighery 14348* (CANB, PERTH); June 2008, *G.J. Keighery & B.J. Keighery 1293* (PERTH); Dec. 1900, *A. Morrison s.n.* (NSW 687848); Nov. 1877, *F. Mueller s.n.* (MEL 0098630); Nov. 1994, *K.L. Wilson, K. Frank, G.J. Keighery & N. Gibson KLW 8895* (NSW, PERTH); May 1995, *K.L. Wilson 9310* (NE, NSW).

Conservation: Conservation status for Western Australian Flora: Declared Rare Flora (Vulnerable); previously believed to be extinct until rediscoved in 1993, (Hopper 1990; Keighery 1993; Brown *et al.* 2008). Twelve populations contain around 1,500 individuals, though fluctuating greatly between fire events. Three populations occur in nature reserves, while nine populations are in state forest or on private land (Department of Environment 2020).

Notes: The lectotype is chosen as it is the only sheet at K annotated with the name *Tetraria australiensis* by Clarke. It is also accompanied by an illustration of a dissected spikelet. While the sheet at K originated at B, no duplicate has been located there and the original B specimen has probably been destroyed.

Tetraria australiensis is sometimes listed as validated by C.B.Clarke in *Bull. Misc. Inform. Kew, Addit. Ser.* 8: 48 (1908), but the name was validly published by Clarke (1904).

Considered to be a fire ephemeral, short-lived and fire-dependant (Evans *et al.* 2003). However, this species can resprout following fire, so it may survive longer than currently thought, as might be expected for a clonal species, but not flower and thus be difficult to locate (Keighery 1993). Monitoring of individuals is required to determine plant longevity.

This species has the common names of Southern Tetraria and Leafy Sedge.

Morelotia gahniiformis Gaudich., *Voy. Uranie Bot.* 4(part 10): 416 (1829), (as *M. gahniæformis*). *Lampocarya gaudichaudii* Brongn. in L.I.Duperrey, *Voy. Monde, Phan.* 2: 166–167, pl. 29 (1833), *nom. illeg. Gahnia gaudichaudii* (Brongn.) Steud., *Syn. Pl. Glumac.* 2: 164 (1855). *Mariscus gaudichaudii* (Brongn.) Kuntze, *Revis. Gen. Pl.* 2: 755 (1891). *Gahnia gahniiformis* (Gaudich.) A.Heller, *Minnesota Bot. Stud.* 1: 802 (1896). *Machaerina gahniiformis* (Gaudich.) J.Kern, *Acta Bot. Neerl.* 11: 223 (1962).

Morelotia gahniiformis Gaudich., *Voy. Uranie, Atlas* (part 4); 4, t. 28 (1827), *nom. inval.*

Type citation: 'In Insulis Sandwicensibus (alt. 450–500 hexap.).'

Type: Hawaii: Iles Sandwich, ouki incolarum, Voy. Uranie, [1819], *C. Gaudichaud-Beaupré s.n.* (lectotype, designated by St John, *Webbia* 13: 334 (1958) as 'holotype': P 00601900*; isolectotypes: G-DC, *n.v.*, K 000881763*, P 00601901*, P 00601902*).

Lamprocarya gaudichii Kunth ex H.Pfeiffer, *Fedde Repert. Sp. Nov.* 23: 349 (1927), *orth. var.*

Gahnia gahniiformis var. *elongata* Kük., *Rep. Nov. Reg. Veg.* 52: 88 (1943).

Type: Hawaii: In volcano Kilauea, May 1909, *U.J. Faurie* 1250 (lectotype, designated by St John, *Webbia* 13: 334 (1958) as 'holotype' B 10 0296673*; isolecto: BM 000991156, P 01727876*, P 01869415*, P 01869423*).

Illustrations: Gaudichaud-Beaupré (1827, t. 28); Brongniart in Duperrey (1833, pl. 29, fig. 5; reproduced by St John 1958 as fig. 1, no. 5); Benl (1937: fig. 6); Benl (1940a: fig. 6); Kern (1962, fig. 1: 1–7); Vanhecke (1974: fig. 57, p. 398); Koyama (1999, pl. 207).

Perennial tufted *herb*, (0.1–)0.2–0.7 m high; plants presumably clonal, 0.3–0.6 m across; rhizome thick, woody, short, branched, 5–8 mm diam., somewhat pseudobulbous; old leaf sheaths covering the rhizome, breaking apart into fibres, usually not twisted at the base with age, pale brown; roots not sand-binding. *Culms* stout, erect, with 1–3 leafy nodes, obtusely trigonous, 1.5–3.8 mm diam., smooth, glabrous, base not enlarged. *Leaves* mostly basal, numerous, and 1–3 cauline; phyllotaxy loosely spirotristichous, sheath margins finely ciliate-scabrous, otherwise glabrous, open, 25–39 mm long, 4–6 mm wide, broader than the leaf lamina, brown or yellowish brown, upper margin membranous, ligule absent; basal leaves 15–45 cm long, 2–8 mm wide, but commonly involute and appearing 1–2.5 mm wide, lamina dorsiventral, ± linear, curved, finely multi-striate,

not scabrid below on midrib, green to yellow-green, slightly paler below, margins scabrous, usually strongly revolute, apex gradually attenuate and curled when dry; cauline leaf lamina 16–28 cm long. *Inflorescence* dense, panicle-like, narrow, linear, (5–)10–35 cm long, 10–25 mm wide, with 3–7 fertile nodes; axis green; bracts leaf-like, rigid, margins scabrid, with pale brown sheaths 10–25(–40) mm long, becoming progressively smaller up the culm, exceeding the spikelet clusters, basal bract usually longer than inflorescence; branches 35–65 mm long, erect, solitary in lower part of inflorescence, the upper ones in groups of 2–4, arising in each bract axil, mostly enclosed in the bract sheath; spikelets on peduncles 0.5–2 mm long; spikelet prophyll present, sheath indistinct, lamina 2.1–2.5 mm long, brown, with 1 distinct vein. *Spikelets* in groups of 2–8, brown, narrow-ovoid, 8–10 mm long, 2–3 mm diam., acuminate, ascending, not compressed, with 6–8 glumes, the topmost infertile, subtended by a minute membranous glume, upper 2 larger glumes each subtending a flower, enclosed by the wing of the next glume, lower flower fertile, bisexual, upper male, reduced and sterile, lower 4–6 glumes empty, glumes distichous, chartaceous, lower glumes caducous, lowest glume 3.8–4.1 mm long, upper glumes 5.6–9.9 mm long, 1.8–3.4 mm wide, hispidulous in upper part, narrowly ovate, acuminate to acute, keeled, with a mucro to 1.5 mm long; rachilla compact, but the uppermost internode elongated and curved in fruiting spikelets. *Perianth segments* absent. *Stamens* 3; anther connective 4.3–9.6 mm long, elongating further after anthesis, linear, persistent at base of nutlet, distal portion held within the convolute apex of subtending glume, so mature nutlets pendent on the inflorescence post-release; anthers yellow, 3.1–4.2 mm long, linear-oblong, base auriculate, with a minutely scabrous apical appendage up to 0.5 mm long. *Style* 3-fid, base 4.6–5.1 mm long, hispidulous, thin throughout, branches 2.5–2.9 mm long, hispidulous. *Nutlet* sessile, ovoid ellipsoid to ellipsoid, subterete but somewhat trigonous, with 3 longitudinal indentations, maturing black, slightly glossy, apex black, not constricted, smooth, 2.7–3.0 mm long including the style base, *c.* 2 mm diam., mesocarp not crustaceous, epidermal cells oblong–square–hexagonal, inconspicuous; style base trigonous-pyramidal, thickened, not corky, persistent, very distinct and cream when immature, indistinct and black when mature, glabrous, *c.* 0.7 mm long; embryo Schoenus-type. Photosynthetic pathway inferred from anatomy to be C_3 (*Henrickson 3490*; *Ordoney, 14 Jul 1940*; Bruhl & Wilson 2007). (Figure 8).

Diagnostic characters: Differs from *M. affinis* in the leaves being more gradually and incompletely revolute; leaf sheath 25–39 (*vs* 35–60) mm long; leaf lamina midrib glabrous (*vs* hairy); spikelets brown (*vs* reddish brown); basal glume 3.8–4.1 (*vs* 2.4–2.8) mm long; fertile glumes hispidulous (*vs* puberulent); the nutlet apex obtuse-apiculate (*vs* subconical), epidermal cells oblong–square–hexagonal (*vs* semi-circular–hexagonal).

Distribution: Endemic to the Hawaiian Islands, present on Kauai, Molokai, Lanai, Maui and Hawaii (Koyama 1990, 1999).

Also reported from Oahu by Kükenthal (1943) based on collections by Macrae and the Wilkes Expedition, but specimens matching the citations have not been located. The lack of recent collections suggests it may now be extinct on Oahu if it was ever present there, but it is more likely that the cited collections were not actually from Oahu, though the Mount Ka'ala is on Oahu, and botanical specimens were collected there by the Wilkes expedition, so the specimen cited would have to have been collected on either Kauai or Hawaii and erroneously labelled. An alternative possibility is that the specimens were in poor condition and thus confused with a species such as *Gahnia beecheyi* H.Mann.

Habitat: Grows on consolidated lava fields, in dry or mesic forest, in lehua-uluhe forest, subalpine shrubland, in bog-like habitats, on steep slopes, and on windswept ridges, at altitudes of 520–2,380 m. Recorded in association with *Antidesma platyphyllum*, *Astelia menziesiana*, *Broussaisia arguta*, *Carex wahuensis*, *Cheirodendron* spp., *Coprosma ernodeoides*, *Deschampsia nubigena*, *Dicranopteris linearis*, *Diospyros sandwicensis*, *Dodonaea viscosa*, *Dubautia dolosa*, *D. menziesii*, *D. platyphylla*, *D. reticulata*, *D. scabra*, *Eragrostis monticola*, *E. variabilis*, *Euphorbia sparsiflora*, *E. remyi*, *Geranium arboreum*, *Kadua* spp., *Lobelia kauaensis*, *Lysimachia hillebrandii*, *L. reayi*, *Lythrum maritimum*, *Machaerina angustifolia*, *M. mariscoides*, *Melicope* spp., *Meterosideros polymorpha*, *M. waialealae*, *Myrsine* spp., *Pelea feddei*, *P. waialealae*, *Perrottetia sandwicensis*, *Polypodium pellucidum*, *Psychotria* spp., *Racomitrium* spp., *Rhynchospora chinensis*, *Rubus niveus*, *Scaevola gaudichaudiana*, *Sophora chrysophylla*, *Sphenomeris chinensis*, *Sticherus owhyhensis*, *Styphelia tameiameiae*, *Tetramolopium capillare*, *Tetraplasandra* spp., *Vaccinium dentatum* and *V. reticulatum*.

Phenology: Flowering possibly bimodal, recorded mainly for June–September and December–January, but apparently sporadic all year round. Fruit mainly recorded for April–June and October–December.

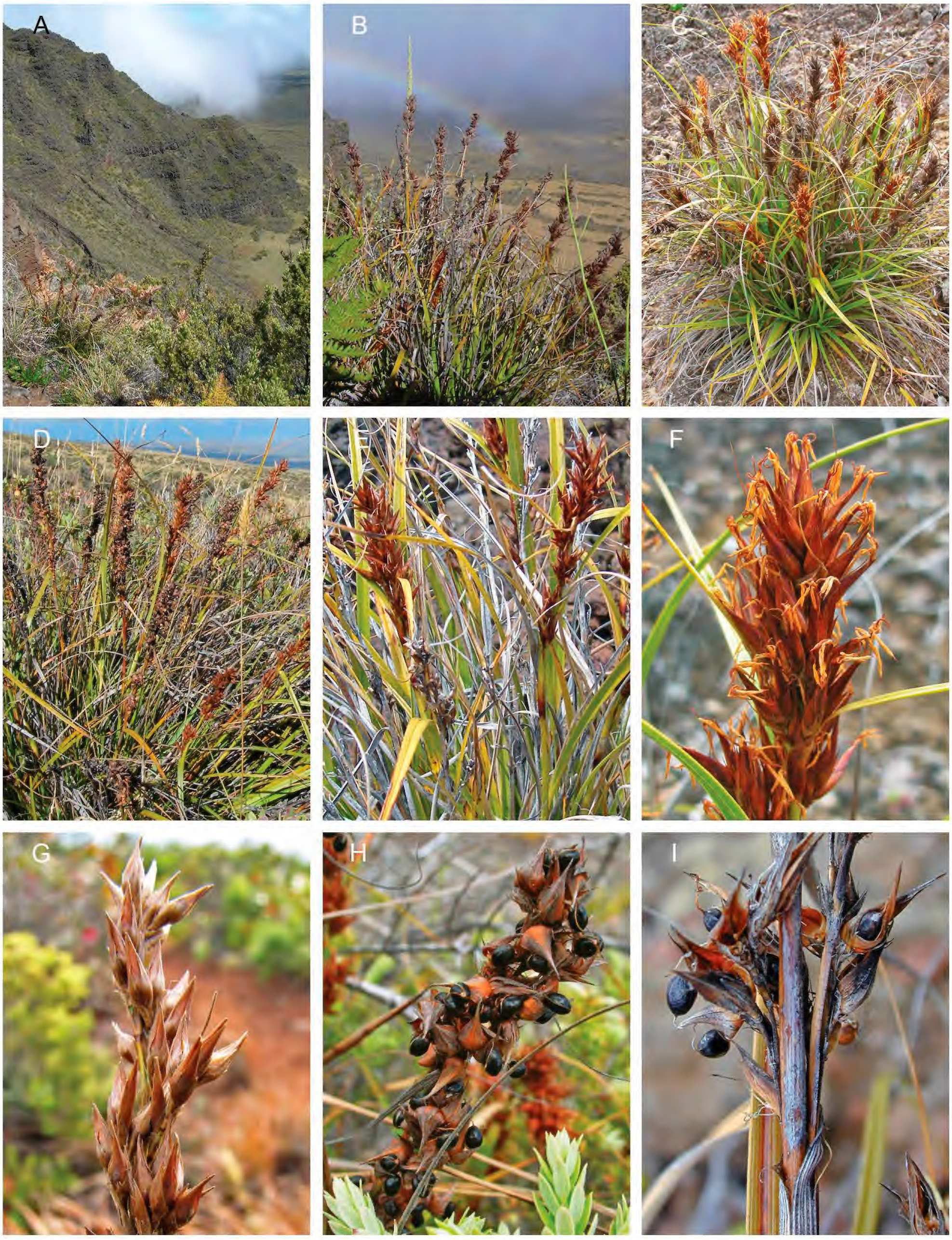

Fig. 8. *Morelotia gahniiformis*. Maui, Hawai'i. A. Habitat. B–D. Habit. E. Inflorescence. F. Inflorescence with old anthers. G. Spikelets in early fruit. H, I. Spikelets with mature nutlets held by persistent anther filaments. Photos by F. & K. Starr. CC-BY 3.0.

Selected specimens examined: HAWAII: HAWAII ISLAND: along Saddle Road 23.5 miles from Hilo, 26 Aug. 1949, *O. Degener, Murashige & Kerr 20210* (BISH, US*); Mauka of Kulani Prison, 8 July 1961, *O. Degener & I. Degener 27833* (K, P*); Junction of Chain-of-Craters and quarry roads, Hawaii Volcanoes National Park, 23 Jan. 1967, *O. Degener 31073* (CBG); along jeep road, Kaupu-lekai Forest Reserve, NW slope of Hualalai, 9 July 1967, *O. Degener, I. Degener & A.B.H. Greenwell 31363* (L, NSW); Galathea Expeditionen, 1845–1847, *D.F. Didrichsen 3371* (BISH, C, NSW, US*); In volcano Kilauea, May 1909, *U.J. Faurie* 1250 bis (P 01869418*);

Kanehaha, Kona, 27 June 1911, *C.N. Forbes 270.H* (BISH, P*); [lava] flow of 1852, NE slope of Mauna Loa, 27 June 1915, *C.N. Forbes 961.H* (BISH, P*, US*); Hawaii Volcanoes National Park, Chain-of-Craters Road, just above Kokoolau Crater, 15 Mar. 1964, *F.R. Fosberg 45158* (US*); 3 miles W of Volcano House in National Park, 6 Aug. 1969, *J.S. Henrickson & L. Johnson 4077* (CSU; NSW); Kilauea, rim of crater, Kilauea Summer Camp, 4 Aug. 1927, *M.C. Neal s.n.* (BISH, P*); Kilauea volcano, Apr. 1911, *J.F.C. Rock & E.W. Giffard s.n.* (BISH, P*); Puu Hualalai, Puuwaawaa, 29 Dec. 1931, *H. St John et al. 11386* (BISH, P*, US); Kahuku parkland, 7 miles NE of Nene Cabin, 24 June 1971, *H. St John 26779* (BISH, NSW); upper Kalapana Trail, 25 June 1959, *B.C. Stone 2965* (BISH, P*). KAUAI ISLAND: Lihu District, Wahiawa headwaters, SE below Kapalaoa, 22 Dec. 2010, *K.R. Wood 14456* (BISH, MBK, NY*, US*). LANAI ISLAND: NW part of Munro Trail, Lanai, *O. Degener, I. Degener & R.W. Hobdy 24306* (NSW, US*); Puheilelu Ridge, Lanai, 13 Aug. 1963, *O. Degener & I. Degener 28328* (K, P*, UPS, US*); Lanai, upper part of mountain, 21 Sept. 1916, *A.S. Hitchcock 14653* (US*); Lanai, 1851–1855, *M.J. Remy 135* (BISH, P*); Lanai, Kaiholena Gulch, SW ridge of Kamoku, 4 Apr. 1947, *H. St John & R.S. Cowan 22607* (BISH, US*). MAUI ISLAND: Manawainui Gulch near Puu Anu, West Maui, 12 July 1927, *O. Degener 8342* (US*); between Red Hill and Kahua, Haleakala, Maui, 24 Nov. 1950, *O. Degener et al. 21110* (NSW); East Maui, east end of Haleakala Crater, 0.5 mile S of Paliiku Cabins, 16 June 1969, *J.S. Henrickson & R. Vogl 3490* (CSU; NSW, US*); Maui, *W.B. Hillebrand s.n.* (B, *n.v.*, MEL, NSW, US*); West Maui, Honokawai Gulch, Aug. 1910, *J.F.C. Rock 8192* (BISH, P*, US*); East Maui, Haleakala, Oct. 1910, *J.F.C. Rock 8518* (BISH, P*, US*); West Maui, Paunau - Kuhua divide, 19 Dec. 1936, *H. St John 17686* (BISH, CBG); Haleakala, slope side Maui, Oct. 1961, *W. Straatmas s.n.* (CANB 717848); W Maui, Hale Pohaku, 24 June 1992, *K.R. Wood & S. Perlean 1974* (US*). MOLOKAI ISLAND: Molokai, upper Kawela, 21 Sept. 1992, *G. Hughes 87* (US*). OAHU ISLAND: [Am Vulcan, *Macrae s.n.*, *n.v.*; Kaala Mountains, *Wilkes Expedition*, *n.v.*, both cited by Kükenthal (1943).] ISLAND UNKNOWN: Iles Sandwich, Voy. Bonite, Sept.–Oct. 1836, *C. Gaudichaud-Beaupré s.n.* (P*); Sandwich Islands, United States Exploring Expedition, 1838–1842, *Wilkes Exploring Expedition s.n.* (US 00426453*).

Conservation: Not threatened, but in some locations (e.g. Waiakeakua), the introduced grasses *Melinis repens* and *Schizachyrium condensatum* and the nitrogen-fixing tree *Morella faya* are crowding out *Morelotia* and other native species (D'Antonio *et al.* 2011), so monitoring should be undertaken. Conserved in a number of nature reserves including Volcanoes National Park. IUCN: Least Concern.

Etymology: Not stated by the author but presumably in reference to the similar form of the plant to species in the genus *Gahnia* J.R.Forst. & G.Forst., and specifically to the Hawaiian species *G. beecheyi*.

Common names: Gaudichaud's sawsedge; 'Uki.

Notes: Five sheets of the type collection of *Morelotia gahniiformis* have been located, which appear to represent a single collection. However, since the protologue is not specific on this, and there are multiple sheets at P, St John (1958) effectively selected a lectotype by differentiating the sheets at P in his publication, specifically using the term holotype in reference to one of the sheets, and physically labelling the sheets as 'holotype' and 'isotypes' respectively. In this case, 'holotype' is to be corrected to 'lectotype' (Art. 9.10; Turland *et al.* 2018).

As noted by St John (1958), there are several fruit of *M. affinis* in a packet on the lectotype sheet (and excluded from the lectotype selection), presumably those used for the illustration in t. XXIX, fig. 4 (Brongniart in Duperrey 1833).

Gaudichaud-Beaupré returned to the Sandwich Islands in Sept.–Oct. 1836 on the *Bonite* and re-collected *Morelotia gahniiformis* at that time, but after the species was named, so these specimens are not type material.

An illustration of *Morelotia gahniiformis* Gaudich. was published in volume 4, Botanique, part 4 of *Voy. Uranie*, on 24 Feb. 1827 (Stafleu and Cowan 1976). The illustration has the species name and numbered parts to the figure, and the figure explanation, which contains considerable detail, published on p. 4 of the same volume. This constitutes 'an illustration with analysis' which would be sufficient to validate the species, but the genus was not already published, and thus the species name is also invalid in this publication (Art. 35.1; Turland *et al.* 2018). Part 10, containing page 416, was published on 18 Sept. 1829 (Stafleu and Cowan 1976) and both the genus and species names are validated there.

Kükenthal (1943) did not designate a particular herbarium holding the type collection of *Gahnia gahniiformis* var. *elongata* Kük. He is known to have examined at least the material now at B and P. St John (1958) effectively selected a lectotype by differentiating the sheets at B and BM in his publication by describing the sheet at B as 'holotype', also physically labelling the sheets as 'holotype' and 'isotypes' respectively. In this case, 'holotype' is to be corrected to 'lectotype' (Art. 9.10; Turland *et al.* 2018). The lectotype (B 10 0296673) has a label with Kükenthal's epithet in his own hand, is in the main collection used by Kükenthal, and it is an ample specimen.

This species has been included under *Gahnia* by some until relatively recently (Koyama 1990, 1999), but is now recognised under *Morelotia* (Bruhl 1990, 1995; Imada 2012).

Morelotia involuta (H.St John) J.J.Bruhl & R.L.Barrett, *Telopea* 24: 176 (2021).

Machaerina involuta H.St John, *Nordic J. Bot.* 4: 57, fig. 1 (1984).

Type: French Polynesia: Austral Islands, Bass Islands, Rapa Island [Rapa Iti], S of Morongota [Morongo Uta *pare* (fort)], 275 m alt., 8 July 1934, *H. St. John & J. Maireau 15434* (holo: BISH 1001238*; iso: BISH 1001239*, BISH 1001240*, BRI AQ0193095*, GH 00050565*, K, NSW 1099912!, NY 4106228*, P 00641812*, P 00641813*, SING 0064504*, US 00512838*).

Illustration: St John (1984; fig. 1).

Perennial tufted *herb*, 0.25–0.6 m high; plants clonal, 0.2–0.5 m across; rhizome thick, woody, short, branched, 10–15 mm diam., not pseudobulbous; old leaf sheaths covering the rhizome, breaking apart into fibres and becoming recurved with age, pale brown to dark brown; roots not sand-binding. *Culms* stout, erect, with 1 leafy node above the middle of the culm, trigonous, 1.3–1.7 mm diam., smooth, glabrous, base not or slightly enlarged. *Leaves* mostly basal, numerous, and 1 cauline; phyllotaxy loosely spirotristichous, sheath glabrous, open, 26–38 mm long, 4–5 mm wide, broader than the leaf lamina, pale brown, upper margin smooth, ligule absent; basal leaves 20–60 cm long, 2.5–4 mm wide, but involute and appearing 1–1.3 mm wide, lamina ±linear, often twisted or curved, finely multi-striate, glabrous, dark green, paler below, margins very finely scabrous, usually recurved, apex gradually attenuate; cauline leaf lamina 15–25 cm long. *Inflorescence* dense, panicle-like, narrow, linear, 10.5–21 cm long, 5–10 mm wide, with 5–8 fertile nodes; axis green; bracts leaf-like, with pale brown sheaths 15–25 mm long, becoming progressively smaller up the culm, exceeding the spikelet clusters, basal bract longer than inflorescence; branches 20–25 mm long, erect, with (1)2 or 3 clustered spikelets on peduncles 0.5–3 mm long, arising in each bract axil; spikelet prophyll present, sheath 3.5–4.2 mm long, brown, with 1 distinct vein, partially enclosing the spikelet, with a slender lamina 1.8–2.1 mm long, brown. *Spikelets* brown, lanceolate, 7–9 mm long, 1.3–1.5 mm diam., ascending, not compressed, with usually 7 glumes, only topmost fertile, bisexual, lower glumes empty, glumes distichous, lowest glume 4 mm long, upper glumes 8–9 mm long, 1.7–2.1 mm wide, glabrous, lanceolate, acuminate, weakly keeled, with a mucro to 3 mm long; rachilla compact and not sinuous in fruiting spikelets. *Perianth segments* present, bristles *c.* 6, inconspicuous, filiform, glabrous, 0.4–1.1 mm long, 1/5–1/3 as long as the nutlet. *Stamens* 3; anther connective 5.1–6.8 mm long, linear, persistent at base of nutlet, distal portion held within the convolute apex of subtending glume, so mature nutlets pendent on the inflorescence post-release; anthers pale yellow, 4–5 mm long, linear-oblong, base auriculate, with a glabrous apical appendage up to 2 mm long. *Style* 3-fid, white, base 3–5 mm long, glabrous, thin throughout, branches 7–10 mm long, hispidulous. *Nutlet* sessile, angular ellipsoid, subterete, but perceptibly 3-sided, mostly stramineous but apex brown and only slightly or not constricted, smooth, 2.1–2.7 mm long including the style base, 0.8–1.0 mm diam., epidermal cells square–hexagonal, but inconspicuous; style base cylindric, hard, persistent, glabrous, *c.* 0.5 mm long and wrinkled when immature, expanding to *c.* 0.7 mm long, smooth and somewhat angular due to continuation of ribs from nutlet; embryo not examined. Photosynthetic pathway not verified. (Figure 9).

Diagnostic characters: Differs from *M. affinis* in: Culms with 1 leafy node (*vs* 0–2(–4) leafy nodes), 1.3–1.7 (*vs* 1.9–3.5) mm diam. Leaf sheath 26–38 (*vs* 35–60) mm long. Basal leaves 2.5–4 (*vs* 4–8) mm wide, but involute and appearing 1–1.3 (*vs* 1.5–2.1) mm wide, margins very finely scabrous, (*vs* harshly scabrous), usually recurved (*vs* strongly revolute) when dry. Inflorescence branches 20–25 (*vs* 20–70) mm long, with (1)2 or 3 (*vs* 3–15) clustered spikelets. Perianth segments present, filiform, 0.4–1.1 mm long (*vs* absent). Nutlet mostly stramineous but apex brown (*vs* lustrous red-brown to black, apex black).

Distribution: Until 2020, only known from three collections made on a single expedition in July 1934, and four collections made in 2002 on Rapa Iti (Rapa Island), in the Austral Islands, French Polynesia. Targeted surveys for the species in March 2020 located seven populations on Rapa Iti where it is apparently endemic (Barrett *et al.* 2021b).

Habitat: Grassy volcanic crests and ridges in open, sunny areas, with *Aristida aspera*, *Asplenium polyodon*, *Athyrium membranaceum*, *Bolbitis lonchophora*, *Callistopteris calyculata*, *Coprosma rapensis*, *Cyathea medullaris*, *Cyperus brevifolius*, *Dryopteris stokesii*, *Dianella intermedia* var. *punctata*, *Dicranopteris linearis*, *Elaphoglossum meyeri*, *Eragrostis brownei*, *Erythrina variegata*, *Eurya rapensis*, *Ficinia nodosa*, *Fitchia rapensis*, *Gahnia aspera*, *Glochidion* species, *Histiopteris incisa*, *Hymenophyllum* sp., *Lycopodiella cernuua*, *Meterosideros collina*, *Peperomia rapensis*, *Pittosporum rapense*, *Rhynchospora stokesii*, *Vaccinium rapense*, and *Veronica rapensis* collected in the vicinity. Introduced taxa recorded in direct association include *Bidens pilosa*, *Miscanthus floridulus* and *Psidium cattleyanum*.

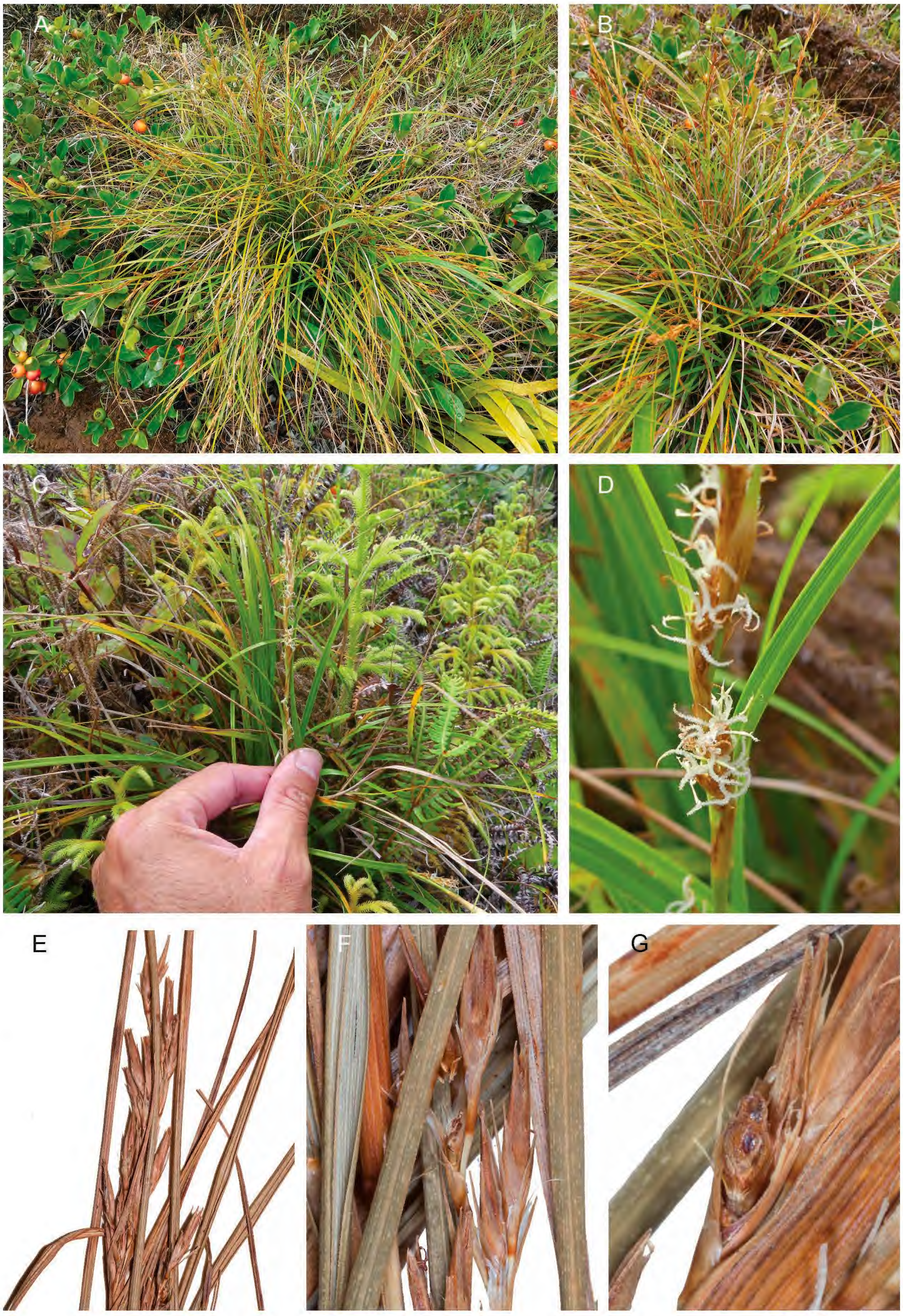

Fig. 9. *Morelotia involuta*. Rapa Iti, French Polynesia. A, B. Habit. C. Leaves and inflorescence. D. Inflorescence with styles. E. Inflorescence. F. Spikelets. G. Fruit in dissected spikelet. A–D from *R. Taputuarai 859, 860* (PAP). E–G from *H. St John 15434* (NSW). Photos: A–D by R. Taputuarai; E–G by R.L. Barrett.

Phenology: Flowers recorded for March and April. Fruit recorded for April and July.

Specimen images examined: French Polynesia: Austral Islands, Bass Islands, Rapa Iti, E slope of Mt Ruatara, 260 m., 9 July 1934, *F.R. Fosberg 11453* (L*, S*, US*), *loc. cit*., 8 July 1934, *F.R. Fosberg 11454* (P*, US*); sentier ver le Mont Maungaoa, 400 m, 21 Mar. 2002, *J-Y. Meyer 1007 & R. Fenstemacher* (PTBG 1000028324*); just west of Area village, 80 m, 19 Mar. 2002, *T.J. Motley 2621 & R. Fenstemacher*, collected by *J.-F.Butaud* (PTBG 1000028319*); Mt. Manguoa (Marugaoa) on ridge just east of Pa (fortress), 380 m, 8 Apr. 2002, *T.J. Motley 2721 & R. Fenstemacher* (PTBG 1000028323*); Hiri Valley, back slopes below Pukumaru Peak, north facing slope, 400 ft, 13 Apr. 2002, *S. Perlman 18062* (PTBG 1000028318*).

Conservation: Poorly known, but native vegetation on Rapa Iti has suffered greatly from human overpopulation in the past and the ongoing presence of feral animals (Prebble and Anderson 2012). In addition, remnant native habitats are commonly heavily invaded by *Miconia calvescens*, *Psidium cattleyanum*, *Rubus rosifolius*, *Hedychium flavescens* and weedy grasses, particularly *Melinis minutiflora*, *Miscanthus floridulus* and several *Paspalum* species (Mueller-Dombois and Fosberg 1998; Meyer 2004; Meyer *et al*. 2015, 2019), and this species is likely to be threatened by habitat loss. It is noted that Brown (1931) did not examine any material of this taxon for his treatment of Cyperaceae the *Flora of Southeastern Polynesia*, despite collections of other Cyperaceae from nearby locations on Rapa, suggesting the species may have already been quite rare at the time of preceding expeditions, though it may have simply been overlooked for the diversity of 'more interesting' species on the island.

Barrett *et al*. (2021b) assessed the conservation status of *Morelotia involuta* following the IUCN (2012) criteria for endangerment as Endangered (EN). The IUCN alphanumeric summary of the evaluation of criteria and subcriteria is: B1b(iii, iv); B2a; B2b(iii); C1; C2a(i); D2.

Etymology: Named from the Latin *involvere* (to roll in) in reference to the involute leaf lamina.

Notes: St John (1984) allied his *Machaerina involuta* to *M. schoenoides* (R.Br.) Koyama [=*Machaerina acuta* (Labill.) J.Kern], a relationship that is only based on superficial morphological similarities.

Most of the fruit on the isotype at NSW are immature, with small style bases, but a few mature fruit are present, with greatly enlarged style bases.

Morelotia microcarpa (S.T.Blake) R.L.Barrett & K.L.Wilson, ***comb. nov.***

Basionym: *Tetraria microcarpa* S.T.Blake, *Proc. Roy. Soc. Queensland* 60: 52 (1949).

Type: Western Australia: South-West Division: 10–20 miles N of Northampton, in sandy heath, 3 September 1947, *S.T. Blake 18138* (holo: BRI; iso: CANB 251338 (2 sheets), K 000960100, L 0042808, MEL 2297586, NSW 687520, PERTH 1049593).

Perennial tufted herb, 0.2–0.4(–0.6) m high; plants clonal, 0.1–0.4 m across; rhizome thick, woody, short, branched, 6–8 mm diam., pseudobulbous; old leaf sheaths covering the rhizome, breaking apart into fine fibres with age, pale brown; roots sand-binding. *Culms* stout, erect, with 1 leafy node, below the inflorescence at least obtusely trigonous, becoming grooved, 1.1–1.3 mm diam., rugulose-asperulous and angles scabrid. *Leaves* mostly basal, numerous, and 1 cauline; phyllotaxy loosely spirotristichous, sheath margins scabrid, otherwise glabrous, 8–30 mm long, 1.5–2.0 mm wide, ± equal width to the leaf lamina, green or pale brown, upper margin membranous, oblique, finely ciliate, ligule absent; cauline sheath tight around culm; basal leaves often exceeding the culms, 16–38(–60) cm long, 2–2.5 mm wide; bases white-membranous, dividing and becoming fimbriate; lamina ± linear, flat or ± complicate, ± flexuous, old leaf tips curling, finely multi-striate, margins scabrid, otherwise glabrous when young, green, concolorous, keeled along mid-nerve, with 3 primary impressed nerves, margins ribbed and finely scabrous, commonly recurved, apex long-attenuate, setaceous; lowest leaves reduced to a sheath, lacking a lamina, pale brown. *Inflorescence* subspiciform panicle-like, narrow, linear, ± flexuous, with 5–7 nodes, 6–15(–25) cm long, 7–10 mm wide, interrupted, axis green or yellow-green, not glaucous; bracts leaf-like, greatly exceeding the spikelet clusters, sheaths in the lower part of the inflorescence open, not enveloping the higher bracts, gradually reducing along the inflorescence, basal bract as long to much longer than inflorescence, to 16 cm long; branches erect, 8–40 mm long, with 12–20 densely clustered (ovoid, head-like, heads 7–10 mm long, 6–7 mm wide), spikelets on short, compressed, scaberulous, peduncles 0.5–3 mm long, arising in each bract axil; spikelet prophyll present, sheath 2.4–2.6 mm long, brown, with 1 distinct vein, partially enclosing the spikelet, with a slender lamina 0.9–1.2 mm long, brown. *Spikelets* dark brown, lanceolate, 3.5–4 mm long, laterally compressed, with usually 6 glumes, only topmost 3 fertile, the lower 2 flowers bisexual but often reduced and infertile, the upper flower bisexual, fertile; glumes distichous, basal glume 1.2–2.2 mm long, upper glumes 2.6–3.4 mm long, 0.7–0.9 mm wide, membranous, brown with

pale red stripes, scabrous on the margins and keel and sparsely scabrous on the lamina, lanceolate, acute to acuminate, with a mucro to 3 mm long, keel distinct; rachilla compact and not or scarcely sinuous in fruiting spikelets. *Perianth segments* 2, thin, minute or absent. *Stamens* 3; anther connective 1.8–2.5 mm long, subulate; anthers yellow, 0.8–0.9 mm long, with a glabrous apical appendage up to 0.2 mm long. *Style* trifid, base 1.8–2.3 mm long, glabrous, slender above, dilated below, branches 1.3–1.5 mm long, hispidulous. *Nutlet* shortly stipitate, broadly obovoid or globular, 1.4–1.7 mm long including the stipe and style base, 0.8–1.2 mm diam., faces smooth, glabrous, epidermal cells square–hexagonal, inconspicuous, cell surface raised so appears very finely papillose at 20× magnification, with three raised, white ribs which broaden above the nut to form the enlarged, thick, persistent, pyramidal or conical style base; embryo not examined. Photosynthetic pathway not examined. (Figure 10).

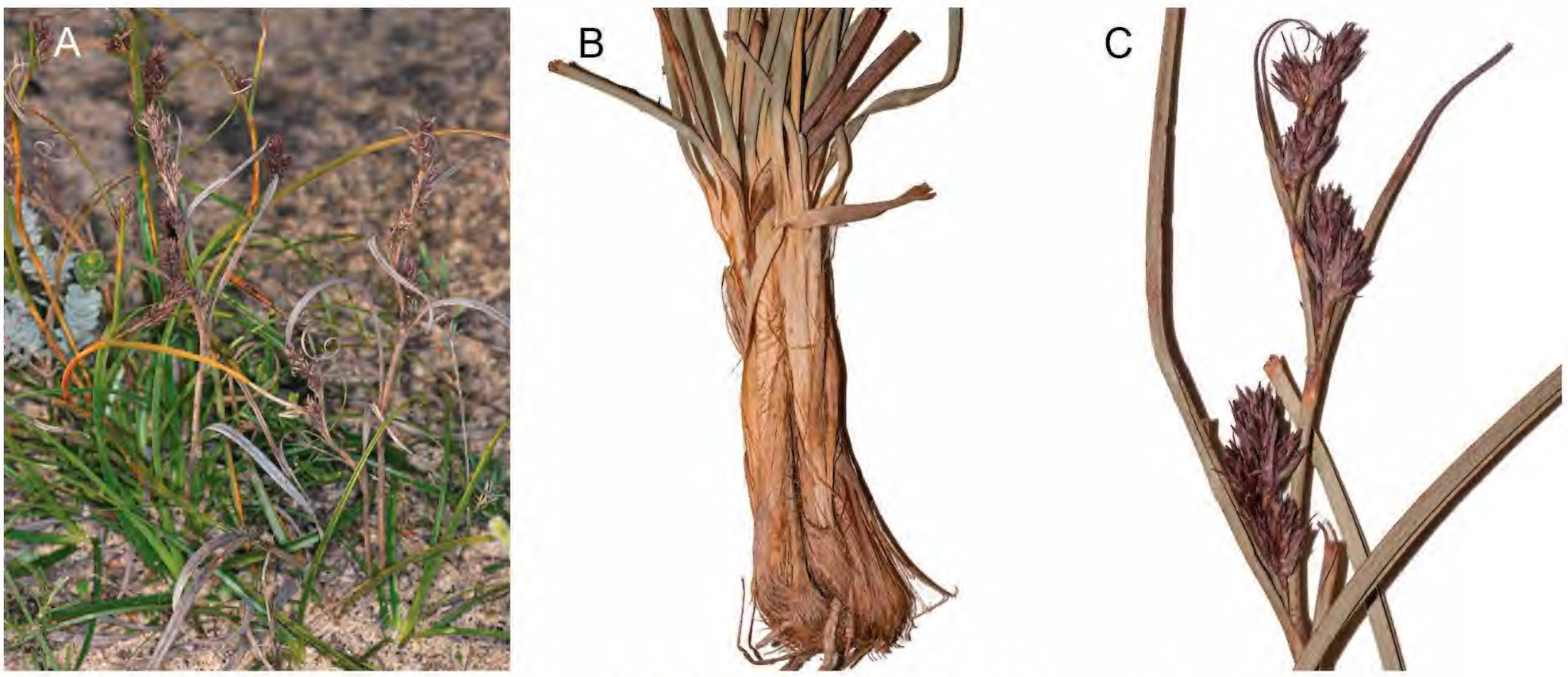

Fig. 10. *Morelotia microcarpa*. A. Habit. B. Plant base. C, D. Infructescence. E, F. Inflorescence. A, D from *R.L.Barrett, M.D. Barrett & C. Karsten RLB 5105* (PERTH); B, C, from *K.L. Wilson 2628* (NSW); E, F, from *J.M. Collins, S. Crees & M. Davis JMC 423* (NSW). Photos by R.L. Barrett.

Diagnostic characters: Differs from *Morelotia octandra* in its much smaller dimensions in all parts; compact rachilla (*vs* sinuous around nutlet); 3 (*vs* usually 8) anthers; glabrous (*vs* hairy) style base and shortly stipitate (*vs* sessile) nutlet base.

Distribution: Endemic to the south-west of Western Australia where it is widespread on the northern sandplain, from north of Kalbarri south and east through the wheatbelt to Cocklebiddy on the edge of the Great Australian Bight, and an apparently disjunct population in the Great Victoria Desert.

Habitat: Recorded in open, low to tall heath, sometimes with scattered mallee eucalypts, on sandplains, sand dunes, sometimes over limestone and gravel in white, grey, brown or yellow sand, sometimes with white or red

clay. Recorded in association with *Acacia acuminata*, *A. latipes*, *A. spathulifolia*, *Acanthocarpus canaliculatus*, *Allocasuarina campestris*, *Amphipogon caricinus*, *Austrostipa macalpinei*, *Baeckea pentagonantha*, *B.* sp. Yuna (M.E.Trudgen 2224), *Banksia prionotes*, *B. sceptrum*, *Blennospora drummondii*, *Bromus arenarius*, *Brunonia australis*, *Calandrinia eremaea*, *Callitris arenaria*, *C. canescens*, *Calothamnus phellosus*, *Calytrix brevifolia*, *C. harvestiana*, *Chamelaucium drummondii*, *Chrysitrix distigmatosa*, *Conospermum stoechadis*, *Dichopogon fimbriatus*, *Ecdeiocolea monostachya*, *E. rigens*, *Enekbatus sessilis*, *Eremaea pauciflora*, *Eucalyptus eudesmioides*, *E. obtusiflora*, *E. oldfieldii*, *Gahnia drummondii*, *Grevillea amplexans*, *G. candelabroides*, *Hakea scoparia*, *Hemigenia scabra*, *Jacksonia velutina*, *Lechenaultia macrantha*, *Lepidosperma tenue*, *Leptospermum erubescens*, *Melaleuca concreta*, *M. stereophloia*, *Mesomelaena preissii*, *M. pseudostygia*, *M. stygia*, *Mirbelia longifolia*, *Monachather paradoxus*, *Netrostylis* sp. Mt Madden (C.D. Turley 40 BP/897), *Pileanthus pedunculatus*, *Rhodanthe manglesii*, *Scaevola spinescens*, *Schoenus caespititius*, *S. clandestinus*, *S. latitans*, *S. racemosus*, *S. subaphyllus*, *S.* sp. G Broad Sheath (K.L.Wilson 2633), *Tersonia cyathiflora*, *Thysanotus patersonii*, *Trachymene pilosa*, *Tricostularia neesii*, *Triodia danthonioides*, *Velleia rosea*, *Verticordia centipeda*, *V. chrysostachys*, *V. spicata*, *Xanthorrhoea* sp. and *Xylomelum angustifolium*.

Phenology: Flowers recorded for August–November. Fruit recorded for September–December.

Selected specimens examined: WESTERN AUSTRALIA: *c.* 6 km along the track to the Z-bend from the intersection with the Ajana-Kalbarri Road, 5 Sept. 1990, *D.E. Albrecht 4216* (NSW); Greenough, Aug. 1903, *C.P.R. Andrews s.n.* (NSW 687522); E side of Wandin Creek, 0.5–1.2 km S of Campbells Road, East Yuna Nature Reserve, *c.* 30 km NW of Mullewa, 19 Sept. 2008, *R.L.Barrett, M.D. Barrett & C. Karsten RLB 5105* (PERTH); *c.* 2 km W of Moore Road on Geraldton–Mt Magnet Road, 20 Oct. 2008, *R.L. Barrett & B.G. Briggs RLB 5274* (PERTH); private property Location number 26758 in remnant E of Magboom Lake, Shire of Goomalling, N of Meckering, 15 Nov. 2007, *J.M. Collins, S. Crees & M. Davis JMC 423* (NSW, PERTH); 9 km W of Kalbarri along road to Highway 1, 1 Oct. 1979, *M.D. Crisp 6294* (CBG, NSW); along State Vermin Fence No. 7, between 45 km and 65 km S of Great Eastern Highway, 5 Nov. 1985, *J. Dodd 254* (CANB, PERTH); 292 km from Mount Magnet on Geraldton Road, 30 Oct. 1963, *D.W. Goodall 2146* (PERTH); Kalbarri National Park, 7 Aug. 1976, *R.J. Hnatiuk 760523* (NSW, PERTH); Cooloomia Nature Reserve, 40 km W of Nerren Nerren Homestead, 69 km N of Kalbarri, 23 Aug. 1983, *S.D. Hopper 3299* (PERTH); Frank Hann National Park, 12 Oct. 1978, *D. Monk 393* (PERTH); Lake Mears Nature Reserve, 15 May 1999, *D.E. Murfet 3543* (AD, PERTH); 11 km SSE of Lake Cairlocup, 16 June 1974, *K.R. Newbey 4218* (PERTH); 23 km S of Tadpole Lake, Frank Hann National Park, *c.* 63 km ENE of Lake King, 21 July 1979, *K.R. Newbey 5380* (NSW, PERTH); 12 km SW of Mount Buraminya, *c.* 40 km WNW of Mount Ragged, 8 Nov. 1980, *K.R. Newbey 8214* (NSW, PERTH); 57 km S of Marvel Loch, 22 July 1981, *K.R. Newbey 8338* (NSW, PERTH); 10.5 km E of Kalbarri, Kalbarri National Park, 24 Oct. 1981, *K.R. Newbey 9363* (NSW, PERTH); 14 km N of Northampton on NW Coastal Highway, 23 Sept. 1976, *T. Whaite & J. Whaite 4173* (NSW); 16 km N of Northampton on Ajana Road, 28 Sept. 1979, *K.L. Wilson 2628* (NSW); 20 km S of Cocklebiddy on track to Twilight Cove, 3 Dec. 1994, *K.L. Wilson 9259* (NSW); North West Coastal Highway, 15 km N of Northampton, 13 Sept. 2012, *K.L. Wilson 10841* (NSW); 13.1 km N of Murchison River (Galena Bridge) on NW Highway, 25 Sept. 2014, *K.L. Wilson & A. Wilson* (MEL, NSW, PERTH).

Conservation: Widespread and not considered threatened. Conserved in Kalbarri National Park, Watheroo National Park, Frank Hann National Park, Lake Mears Nature Reserve and Nuytsland Nature Reserve.

Notes: This relatively diminutive species remains poorly known as it grows in areas with low rainfall and many of the collections are not in good fertile condition, having only old inflorescences. Further assessment of regional variation is recommended once more collections become available, particularly from the southern and eastern extent of its range.

Morelotia octandra (Nees) R.L.Barrett & J.J.Bruhl, ***comb. nov.***

Basionym: *Elynanthus octandrus* Nees, *Ann. Mag. Nat. Hist.* 6: 48 (1841)

Tetrariopsis octandra (Nees) C.B.Clarke, *Bull. Misc. Inf., Kew – Add. Ser.* 8: 45 (1908). *Schoenus octandrus* (Nees) F.Muell., *Fragm.* 9(73): 31 (1875). *Tetraria octandra* (Nees) Kük., *Repert. Spec. Nov. Regni Veg.* 29: 193 (1931).

Type citation: “ad flumen Cygnorum lectae. Drummond.”

Type: Western Australia: Swan River [colony], 1839, *J. Drummond s.n.* (holotype: CGE; isotype: K 000960098!); possible isotype: Western Australia: *J. Drummond 939* (MEL 2203859).

Elynanthus revolutus Nees ex Lehm., *Nov. Stirp. Pug.* 8: 54 (1844).

Type citation: “Habitat in locis glareosis inter frutices montis Greenmountain (Perth.). (Herb. Preiss. no. 1769.)”

Type: Western Australia: Greenmount Hill, near Perth, 26 Apr. 1840, *L. Preiss* [*Plantae Preissianae No. 1769*] (holotype: LD 1732179!).

Tetrariopsis octandra C.B.Clarke in L.Diels & E.Pritzel, *Bot. Jahrb. Syst., Pflanzenges. Pflanzengeog.* 35(1): 81 (1904), *nom. inval.*

Illustrations: Clarke (1909: tab. LXXXI(5), p. 81); Metcalfe (1971; fig. 65e, f); Dell and Bennett (1986: fig 65j); Bruhl (1995; fig. 6.4); Scott and Negus (2002: fig. 3, p. 23); Wheeler and Graham (2002: fig., p. 298); Barrett and Tay (2015: pl. 1–3, p. 203); Keeble (2017, pl. p. 81).

Perennial tufted herb, 0.7–1.2 m high; plants clonal, 0.2–0.8 m across; rhizome thick, woody, short, branched, 10–15 mm diam., pseudobulbous; old leaf sheaths covering the rhizome, breaking apart into fibres with age, dark brown to blackish brown; roots sand-binding. *Culms* stout, erect, with none or 1 leafy node, ± terete at the base but very obtusely 3-angled below and within the inflorescence, 1.0–3.5 mm diam., multi-striate, glabrous. *Leaves* mostly basal, numerous, and with none or 1 cauline; phyllotaxy loosely spirotristichous, sheath glabrous, tight around culm, 18–35 mm long, 1–3 mm wide, ± equal width to the leaf lamina, dark brown to blackish brown, upper margin with fine, blunt scabrous projections, ligule absent; basal leaves 15–60 cm long, 2–4 mm wide, lamina ± linear, often twisted or curved, finely multi-striate, glabrous, dark green, slightly paler below, margins finely bluntly scabrous, revolute, apex long-attenuate. *Inflorescence* open, panicle-like, narrow, linear to lanceolate, 13–35 cm long, 10–20 mm wide, axis green, not glaucous; with 3 or 4 nodes; bracts leaf-like, becoming progressively smaller up the culm, ± equal to greatly exceeding the spikelet clusters, basal bract usually shorter than inflorescence; branches erect, with 2 or 3 clustered spikelets on peduncles 0.5–5 mm long, arising in each bract axil; spikelet prophyll present, sheath 3.2–4.5 mm long, brown, with 3 distinct veins, partially enclosing the spikelet, with a slender lamina 2.1–8.5 mm long, green. *Spikelets* chestnut to brown, ovate, 10–15 mm long, not compressed, with usually 7, rarely 9, glumes, upper glume with a sterile male flower, second upper glume bisexual fertile, lower glumes empty (?rarely the 3rd upper glume with a bisexual sterile flower), glumes spirodistichous, basal glume 5.0–7.8 mm long, fertile glumes 7.2–11.5 mm long, 1.8–2.9 mm wide, scabrous to pubescent, especially on keel and towards the apex, elliptic-lanceolate, acute to acuminate, weakly keeled, with a mucro 0.5–1.0 mm long; rachilla compact and only shortly sinuous around nutlet in fruiting spikelets. *Perianth segments* absent. *Stamens* (4 or 6)8(9); anther connective 5.3–8.4 mm long, linear; anthers pale yellow, 4.4–6.2 mm long, linear-oblong, base auriculate, with a glabrous apical appendage up to 1.4 mm long. *Style* 3–5-branched, base 5.5–7.3 mm long, finely scabrous, thin above, dilated below, branches 2.5–3.3 mm long. *Nutlet* pale brown, sessile, angular globose, strongly 3–5-ribbed, 4.5–5.1 mm long including the style base, 1.6–1.8 mm diam., epidermal cells square–hexagonal, but inconspicuous; apex with a very distinct persistent style base, depressed-ovoid, somewhat constricted at the base, scabrous-pubescent, 1.5–2.0 mm long; embryo not examined. Photosynthetic pathway inferred from anatomy to be C_3 (*Blake 2240*; *Seabrook 130*; *P.G. Wilson 3965*; Bruhl & Wilson 2007). 1C = 0.23 pg (*R.L. Barrett RLB 7787*; Bureš *et al.* 2013). (Figure 11).

Diagnostic characters: Differs from *Morelotia australiensis* in its 0 or 1 (*vs* 3 or 4) nodes below the inflorescence; glabrous (*vs* pubescent) leaf sheath; leaf lamina 15–60 (*vs* 12–18) cm long; spikelets 10–15 (*vs* 8–10) mm long; 7–9 scabrous to pubescent (*vs* 5 glabrous) glumes; rachilla curved around the nutlet (*vs* compact); and usually 8 (*vs* usually 6) anthers.

Distribution: Endemic to the south-west of Western Australia where it is relatively common but scattered in near-coastal areas from Eneabba on the northern sandplains, Swan Coastal Plain and the Darling Scarp, south to Albany.

Habitat: Variously recorded on coastal sandplains, in sandy heath, lateritic gravelly sand, in sandy clay loam over laterite, in woodland, red clay loam, winter wet loam over granite, and on slopes with outcropping granite. Recorded in association with *Allocasuarina fraseriana*, *A. humilis*, *Ammothryon grandiflorum*, *Anigozanthos manglesii*, *Astroloma ciliatum*, *Banksia attenuata*, *B. coccinea*, *B. grandis*, *B. ilicifolia*, *B. menziesii*, *B. sessilis*, *Burchardia congesta*, *Caesia micrantha*, *Caustis dioica*, *Corymbia calophylla*, *Eremaea pauciflora*, *Eucalyptus marginata*, *Lepidosperma* spp., *Lyginia imberbis*, *Macarthuria australis*, *Mesomelaena pseudostygia*, *Morelotia australiensis*, *Schoenus benthamii*, *Stylidium carnosum*, *Thysanotus sparteus*, *Xanthorrhoea brunonis* and *X. preissii*.

Persistent in the landscape due to its clonal growth, with individuals tracked for over 30 years in Kings Park, Perth, and observed to resprout very quickly post-fire (Baird 1977).

Phenology: Flowers recorded for May–November. Fruit recorded for October–December.

Fig. 11. *Morelotia octandra*. A. Habit. B. Plant base with leaves. C. Leaf sheaths showing rhizome section. D–F. Inflorescence. G, H. Spikelets with fresh anthers. I. Spikelets with styles. A, D–G from *R.L. Barrett RLB 7787* (PERTH); B from *K.L. Wilson 3045* (NSW); C from *H. Salasoo 4147* (NSW). Photos A–G by R.L. Barrett; H, I by K.R.Theile.

Selected specimens examined: WESTERN AUSTRALIA: West of Mount Barker, 30 Sept. 1970, *A.M. Ashby 3651* (AD, NSW, PERTH); Hi Vallee Farm, Property of D. & J. Williams, N side of Tootbardie Road, *R.L. Barrett & B.G. Briggs RLB 5251A* (PERTH); Kings Park, Perth, 17 July 2012, *R.L. Barrett RLB 7787* (PERTH); 12 km from Manypeaks along Highway 1 towards Jerramungup, 13 Jan. 1979, *M.D. Crisp 5084* (CBG, NSW); Kamballup Rubbish Reserve, Woogenellup Rd, Kamballup, 12 Aug. 1997, *E.J. Croxford 7771* (PERTH); 10 km N of Wandering, 5 Dec. 1996, *R. Davis 1660* (PERTH); 700 m N along Yarra Road from junction of Brookton

Highway, 22 Feb. 2001, *R. Davis 9533* (PERTH); Kalamunda, 19 km E of Perth, 2 Aug. 1985, *R. Hamilton & M. Hamilton 141* (MEL, NSW, PERTH); Hi Vallee property, Warradarge, 9 July 1999, *M. Hislop 1334* (PERTH); Mount Frankland National Park, 36.1 km S of Shannon along Western Highway, 7 Oct. 2003, *J. Hodgon 795* (NE, NSW); Bow River, Jan. 1913, *S.W. Jackson s.n.* (K, NSW); western side of Mount Manypeaks, 40 km E of Albany, 20 July 1986, *G.J. Keighery 8218* (CANB, PERTH); Wooroloo, Sept. 1907, *M. Koch 1641* (K); slope above W bank of Helena River, *c.* 9.5 km WNW of Mundaring Weir, 2 Sept. 1995, *B.J. Lepschi 1950* (CANB, PERTH); 25 km NNE of Jurien, 24 Sept. 1981, *K.R. Newbey 9394* (CANB, NSW, PERTH); Swan River, Mount Eliza [Kings Park], Perth, June 1839, *L. Preiss* [*Plantae Preissianae No. 1770*] (HBG, K, LD, MEL); sandy woodland between the town of Perth and the city of Fremantle, Dec. 1838, *L. Preiss* [*Plantae Preissianae No. 1771*] [excl. piece of *Lepidosperma gladiatum*] (LD); Perth suburb Daglish, 23 Sept. 1970, *H. Salasoo 4147* (NSW); Witchcliffe townsite, 15 Sept. 2001, *J. Scott 433* (PERTH); Hawkesvale Bushland Conservation Area, Hazelmere, 11 Aug. 2007, *K.R. Thiele 3321* (PERTH); 8 km NE from Midland on Toodyay Road, 14 Sept. 1976, *T. Whaite & J. Whaite 4107* (NSW); Walpole-Nornalup National Park, track to Blue Holes, 13 Aug. 1992, *J.R. Wheeler 3165* (PERTH); 1.5 km from Chester Pass Road on Stirling Range Drive, 19 Oct. 1979, *K.L. Wilson 2995* (NSW); Three Chain Road, 3.5 km W of McGregor Road towards Scott River Road, 21 Oct. 1979, *K.L. Wilson 3045* (NSW); Gales Road, Ambergate, 22 Oct. 1979, *K.L. Wilson 3062* (NSW); 12 km S of Busselton, Ambergate Regional Park, Darling District, 14 Nov. 1994, *K.L. Wilson, K. Frank, G.J. Keighery & N. Gibson KLW 8896* (NSW, PERTH); Clackline–Toodyay road, *c.* 7.4 km N of Great Eastern Highway, 22 Sept. 2014, *K.L. Wilson 11169* (NSW); 7 km E of Mt. Barker, 19 Sept. 1964, *P.G. Wilson 3363* (AD, PERTH); 28 km S of Collie, 14 Dec. 1965, *P.G. Wilson 3965* (CANB, NSW, PERTH).

Conservation: Widespread and well conserved, including in Kings Park, Porongurup National Park and Stirling Range National Park. IUCN: Least Concern.

Notes: Clarke (1908) created a new genus *Tetrariopsis* for this species, relating it to *Elynanthus* (then incorporating *Tetraria*, now a synonym of *Schoenus*) on the basis of spikelets with 7 glumes, 2-flowered spikelets, the short rachilla, perianth absent, stamens 8, styles 3–5-fid and nutlets globose, with 3–5 ribs and a depressed-ovoid persistent style base. Kükenthal (1931) gave a detailed discussion on the morphological affinities and differences between *Tetraria*, *Tetrariopsis* and *Macrochaetium* Steud. (=*Cyathocoma* Nees). Kükenthal (1931) dismissed the shape of the spikelets and glumes as not significantly different to *Tetraria*, and identified the sexuality of the flowers as the key feature to be assessed. Kükenthal (1931) found that the upper flower in *Tetrariopsis* is bisexual, but usually only male fertile, and the second flower bisexual fertile, the reverse arrangement to *Tetraria*. However, some spikelets were found to have two bisexual fertile flowers, and some with only 4 anthers. A single specimen (*Diels 2513*) from the Serpentine River had the upper flower bisexual fertile, and the lower flower infertile, but we have not been able to find material of this collection and while it may be correct, it cannot be ruled out that this may have been *Morelotia australiensis*. Exceptions to the general pattern in *Tetraria* were claimed for *T. cuspidata* (Rottb.) C.B.Clarke (=*Schoenus cuspidatus* Rottb.), *T. bachmannii* Kük. (=*Cyathocoma bachmannii* (Kük.) C.Archer) and *T. thuarii* P.Beauv. (=*Schoenus compar* L.), but none of these species remains in *Tetraria* as defined here.

The type material at CGE and K has no collection number (*J. Drummond s.n.*). There is a specimen at MEL (MEL 2203859) that is a possible isotype (*J. Drummond 939*) as Drummond's collection numbers were commonly omitted or lost when labels were transcribed and we have found no evidence that Drummond collected this species twice.

Tetraria P.Beauv., *Mem. Inst. Fr.* 16: 54 (1816), *nom. cons. prop.* (see Larridon *et al. Taxon* 66: 1226, 2018).

Type species: *Tetraria thermalis* (L.) C.B.Clarke, *typ. cons. prop.* (see Larridon *et al. Taxon* 66: 1226, 2018).

Schoenopsis P.Beauv. ex T.Lestib., *Essai Cypér.* 34 (1819).

Type species: *Schoenopsis flexuosa* (Thunb.) Nees, designated by Larridon *et al. S. Afr. J. Bot.* 118: 21 (2018).

Lepisia C.Presl, *Lepisia* (preprint 1829); *Symb. Bot.* 1: 9 (1830). *Tetraria* sect. *Lepisia* (C. Presl) C.B.Clarke, *Bull. Misc. Inform. Kew, Addit. Ser.* 8: 126 (1908).

Type species: *Lepisia ustulata* (L.) C.Presl.

Sclerochaetium Nees, *Linnaea* 7: 511 (1832).

Type species: *Sclerochaetium thermale* (L.) Nees, designated by Larridon *et al. S. Afr. J. Bot.* 118: 22 (2018).

Aulacorhynchus Nees, *Linnaea* 9: 305 (1834). *Tetraria* sect. *Aulacorhynchus* (Nees) C.B.Clarke, *Bull. Misc. Inform. Kew, Addit. Ser.* 8: 126 (1908).

Type species: *Aulacorhynchus crinifolius* Nees.

Boeckeleria T.Durand, *Index Gen. Phan.* 504 (1888). *Decalepis* Boeckeler, *Bot. Jahrb. Syst.* 5: 509 (1884), *nom. illeg.*

Type species: *Decalepis dregeana* Boeckeler.

Lophoschoenus Stapf, *J. Linn. Soc., Bot.* 42: 179 (1914).

Type species: *Lophoschoenus arundinaceus* (Sol. ex Vahl) Stapf.

Perennial tufted herbs, 0.3–3.0 m high; plants clonal, compact to open, clones 0.2–2 m across; rhizome thick, woody, short, branched, 1–45 mm diam., non-pseudobulbous; old leaf sheaths covering the rhizome, breaking apart into fine fibres with age, reddish brown to dark brown; roots sand-binding. *Caudex* absent or present. *Culms* slender to stout, rigid, erect to spreading or sometimes arcuate, 30–150 cm long below inflorescence, with 0–5 nodes, terete or trigonous, usually finely striate, 0.5–8 mm diam., glabrous, green, base not enlarged. *Leaves* mostly basal, numerous, and 0–5 cauline; phyllotaxy loosely spirotristichous; sheath 18–82(–92) mm long, 1.0–1.9 mm wide, broader or narrower than the leaf lamina, margins rapidly breaking apart, glabrous or ciliate, chestnut-brown or brown, often shiny, upper margin narrowly membranous, oblique to truncate, ligule absent; cauline sheath tight or loose around culm, brown or dark brown to black; *pseudopetiole* usually obscure or absent; leaves usually not exceeding the culms, lamina dorsiventral, 6–100 cm long, 0.5–24 mm wide; bases not differentiated; lamina ± linear, flat, involute or channelled throughout and commonly ± V-shaped in section, ± flexuous, old leaf tips not or sometimes curling, finely multi-striate, lamina usually glabrous, green to yellow green, ± concolorous, often strongly keeled along mid-nerve, margins very finely scabrous, usually entire but sometimes denticulate, flat to involute, apex long-attenuate; lowest leaves usually not reduced to a sheath. *Inflorescence* dense to open, but usually elongate panicle-like (sometimes sub-capitate), usually narrow, ± linear to lanceolate, ± erect or sometimes arcuate, with 1–11 nodes, 6–80 cm long, 0.8–10 cm wide, interrupted to ± continuous, axis green to yellow-green, not glaucous; bracts usually reduced leaf-like at the base, usually bract-like with a slender lamina above, usually exceeding the branchlets, sheaths open, not enveloping the higher bracts, gradually reducing along the inflorescence, basal bract usually somewhat shorter than to exceeding inflorescence, 6–50 cm long; basal branchlets 2.5–20 cm long, 1 or 2 arising in each bract axil; branches erect, each with 1–6 spikelets, spikelets solitary or appearing paired on compressed, scabrous-margined peduncles 0.5–15 mm long. *Spikelet prophyll present*, sheath 1.3–16 mm long, brown, midrib distinct, partially enclosing the spikelet, with a slender lamina 0.3–7.5 mm long, brown. *Spikelets* 3–100+ per inflorescence, brown, elliptic to lanceolate, 4.7–25 mm long, 1.1–3.7 mm wide, subterete, 5–9 glumes, only topmost 2 or 3 fertile, lower flower bisexual, functionally male, upper 1 or 2 bisexual, fertile, usually no reduced glume above the florets (present in *T. cernua*); glumes distichous, basal glume 1.1–15 mm long, fertile glumes 4.1–15 mm long, 0.8–3.5 mm wide, membranous, brown or red-brown, glabrous or ciliate on the keel, margins translucent and often minutely ciliate, lamina glabrous to minutely scabrid, ovate, acute, usually with a mucro 0.5–12 mm long, keel sometimes distinct only towards the apex; rachilla compact and not sinuous in fruiting spikelets. *Perianth segments* absent or 6, whitish, 0.4–5 mm long, *c.* one quarter to as long as the nutlet, base not usually dilated, filiform to subulate, tapering to a fine point, margins glabrous or scabrous. *Stamens* 3; anther connective 3.4–16 mm long, subulate; anthers yellow, 2.3–3.8 mm long, with a glabrous or scaberulous apical appendage 0.4–1.1 mm long. *Style* 3- or 4-fid, base 2.7–9 mm long, slender and usually hispidulous in upper half, slender to slightly enlarged and glabrous in lower half, branches 1.6–10 mm long, hispidulous. *Nutlet* distinctly stipitate, constricted, obovoid to broad-ellipsoid, obscurely trigonous, usually dull, pale brown to dark brown, 1.3–11 mm long including the stipe and persistent portion of the style base, 0.5–4.5 mm diam., faces ± smooth (can appear finely papillose) or tuberculate, glabrous, epidermal cells ± oblong to ovate, inconspicuous, with 3 or 4 fine white ribs, style base not or slightly enlarged, thick, persistent, cap-like to shortly pyramidal; embryo Schoenus-type. Photosynthetic pathway C_3.

Diagnostic characters: Differs from *Morelotia* in having distinctly stipitate nutlets (*vs* ± sessile, or shortly stipitate in *M. microcarpa*). The leaf sheaths are usually much more divided in *Tetraria* species, though they can be somewhat divided in some *Morelotia* species.

Distribution: Most species are endemic to southern Africa, with seven species endemic to New Caledonia, and one in Borneo.

Notes: The delimitation of *Tetraria* has been problematic for most of its history (Clarke 1894, 1897–1898; Kükenthal 1940; Levyns 1947, 1950; Compton 1976; Browning and Gordon Gray 1995a, b; Slingsby and Verboom 2006; Verboom 2006; Viljoen *et al.* 2013; Slingsby *et al.* 2014; Muasya 2016; Browning and Goetghebeur 2017; Larridon *et al.* 2018b). A refined delimitation has been provided by Larridon *et al.* (2018b) that includes about 39 species. One *Tetraria* species from Asia awaits transfer to another genus (R.L. Barrett & I. Larridon, unpubl. data), following the removal of all Australian species formerly included in *Tetraria* by Barrett *et al.* (2021b) and in this paper.

The generic description above is based primarily on the four species treated here in detail, and while they were chosen to represent the greatest range of morphological diversity in the genus, it is likely that some modification to the generic description will be required once all species have been examined in detail. At least four of the South African species require taxonomic revision (G.A. Verboom *pers. comm.*).

A key to *Tetraria* species is not provided as only selected species have been examined for this study. Most South African species are keyed out in Kükenthal (1940), Raynal (1974) provides a table of diagnostic characters for the New Caledonian species, and Kern (1974) describes the Asian species.

Tetraria arundinacea (Sol. ex Vahl) T.Koyama, *J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot.* 8: 74 (1961).

Schoenus arundinaceus Sol. ex Vahl, *Enum. Pl. Obs.* 2: 220 (1805). *Carpha arundinacea* (Sol. ex Vahl) Brongn., *Voy Monde* 2: 169, t. 30 (1829). *Chaetospora arundinacea* (Sol. ex Vahl) A.Dietr., *Sp. Pl.* 2: 31 (1833). *Asterochaete arundinacea* (Sol. ex Vahl) Kunth, *Enum. Pl.* 2: 312 (1837). *Cyclocampe arundinacea* (Sol. ex Vahl) Benth. in G.Bentham & J.D.Hooker, *Gen. Pl.* 3: 1063 (1883). *Lophoschoenus arundinaceus* (Sol. ex Vahl) Stapf, *J. Linn. Soc., Bot.* 42: 180 (1914). *Costularia arundinacea* (Sol. ex Vahl) Kük., *Repert. Spec. Nov. Regni Veg.* 44: 185 (1938).

Type citation: 'Schoenus radiatus. *Forst. prodr. n.* 491.' '*Habitat in* nova Caledonia. *Frabricius Professor Kilonensis*.'

Type: 'Habitat in Nova Caledonia' 'Hb. Vahlian. Coll. Forst. ded. Dr. Fabri.' [New Caledonia: Balade, 5–13 Sept. 1774, *J.R. Forster, J.G.A. Forster & A. Sparrman s.n.*] (holotype: C 10010116 [ex Herb. Vahl]*, iso: B W01117-010 [*Willdenow Herbarium No. 1117*]*, BM 000798904*, BM 000798905*, BM 000991058*, BM 000991059*, K 000960113).

Costularia daenikeri Kük., *Repert. Spec. Nov. Regni Veg.* 46: 31 (1939). *Tetraria daenikeri* (Kük.) T.Koyama, *J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot.* 8: 74 (1961).

Type citation: 'Neu-Kaledonien: In grasreichem Gebüsch, auf dem Serpentinblockgrat südöstlich des Mt. Humboldt-Gipfels, XI. 1924 (Däniker n. 552!).

Type: New Caledonia: Mount Humboldt, 7 Nov. 1924, *A.U. Däniker 552* (holotype: B, presumed destroyed; isotypes: P 00607409, fragment*, Z 000005206*).

[*Schoenus arundinaceus* Sol. ex G.Forst., *Fl. Ins. Austr.* 89 (1786), *nom. inval., nom. nud.*; *Schoenus radiatus* J.R.Forst. ex Vahl, *Enum. Pl. Obs.* 2: 220 (1805), *nom. inval., in syn., non* L.f. (1782), probably in error for *S. arundinaceus*.]

Illustrations: Brongniart in Duperrey (1833, t. 30); Hooker and Hooker, (1883 t. 1434); Kaphahn (1905; figs 8–10); Clarke (1909; t. 79, figs 1–4); Metcalfe (1971; fig. 48d); Raynal (1974; fig. 7, 1–5); Wulff *et al.* (2010; p. 258, pl., p. 260, pl.).

Perennial tufted herb, 1.5–3.0 m high; plants clonal, with distant culms, clones 0.5–3 m across; rhizome thick, woody, long, branched, 15–20 mm diam., not pseudobulbous; old leaf sheaths covering the rhizome, breaking apart into fine fibres with age, reddish brown to dark brown; roots sand-binding. *Caudex* erect, to 70 cm high, 15–23 mm diam., with a loose rosette of many leaves towards the apex, old leaves persistent below. *Culms* stout, rigid, erect, with 3 or 4 nodes, trigonous, often deeply grooved, 3–7 mm diam., smooth, glabrous, green to yellow-green, base not enlarged. *Leaves* mostly at apex of the caudex, numerous, and 3 or 4 cauline; phyllotaxy loosely spirotristichous; sheath 45–65 mm long, 4–8 mm wide, slightly narrower than the leaf lamina, margins scabrid, otherwise glabrous, pale brown, shiny, upper margin not membranous, truncate, ligule absent; cauline sheath tight around culm; *pseudopetiole* obscure or absent; rosette leaves long, but not exceeding the culms, lamina dorsiventral, 40–100 cm long, 5–10 mm wide; bases not differentiated, not dividing; lamina ± linear, ± V-shaped in section, particularly channelled towards the apex, ± flexuous, old leaf tips not curling, finely multi-striate, lamina glabrous, mostly green but yellow just above the sheath, ± concolorous, not keeled along mid-nerve, margins slightly denticulate and finely scabrous, prominently recurved, apex long-attenuate; lowest leaves not reduced to a sheath. *Inflorescence* elongate, panicle-like, narrow but somewhat spreading, ± erect, with 6–11 nodes, 30–70 cm long, 5–10 cm wide, interrupted, axis green or yellow-green, not glaucous; bracts reduced leaf-like at the base, bract-like with a slender lamina above, not exceeding the branchlets, sheaths open, not enveloping the higher bracts, gradually reducing along the inflorescence, basal bract much or somewhat shorter than inflorescence, 15–50 cm long; basal branchlets 7–20 cm long; branches erect to shortly spreading, elongate, with secondary and tertiary fascicles of branchlets, each with 2–6 spikelets, spikelet(s) solitary or paired on short, compressed, scabrous-margined peduncles 0.5–4.5 mm long, arising in each bract axil; spikelet prophyll present, sheath 1.1–2.0 mm long, brown, midrib distinct, partially enclosing the spikelet, with a slender lamina 0.2–0.6 mm long, brown. *Spikelets* brown, oblate to lanceolate, 4.7–6.6 mm long, subterete, with 6–9 glumes, only topmost 2 fertile, both bisexual, fertile, no reduced glume above the florets; glumes subdistichous, basal glume 1.1–1.9 mm long, fertile glumes 4.1–5.3 mm long, 1.1–1.7 mm

wide, membranous, red-brown, glabrous on the keel, margins ciliolate, lamina glabrous, ovate-lanceolate, subacute, with a mucro to 0.5 mm long, keel distinct; rachilla compact and not sinuous in fruiting spikelets. *Perianth segments* 6, whitish, 3.3–4.4 mm long, *c.* twice as long as the nutlet, base not dilated, tapering to a fine point, margins finely and densely scabrous. *Stamens* 3; anther connective 3.4–3.9 mm long, subulate; anthers yellow, 2.3–2.7 mm long, with a glabrous apical appendage up to 0.4 mm long. *Style* trifid, base 3.4–4.1 mm long, slender and glabrous above, dilated and densely scabrous in lower third, branches 1.6–1.9 mm long, hispidulous. *Nutlet* indistinctly stipitate, slightly constricted, obovoid to ellipsoid, obscurely trigonous, dull, mid-brown, 1.3–1.7 mm long including the stipe and persistent portion of the style base, 0.5–0.7 mm diam., faces smooth, puberulous near apex, epidermal cells ± oblong to ovate, inconspicuous, with three fine white ribs, style base slightly enlarged, thick, persistent, shortly conical; embryo not examined. *Photosynthetic pathway* inferred from anatomy to be C_3 (Bruhl & Wilson 2007; *Raynal & Jaffré 16508*). (Figure 12)

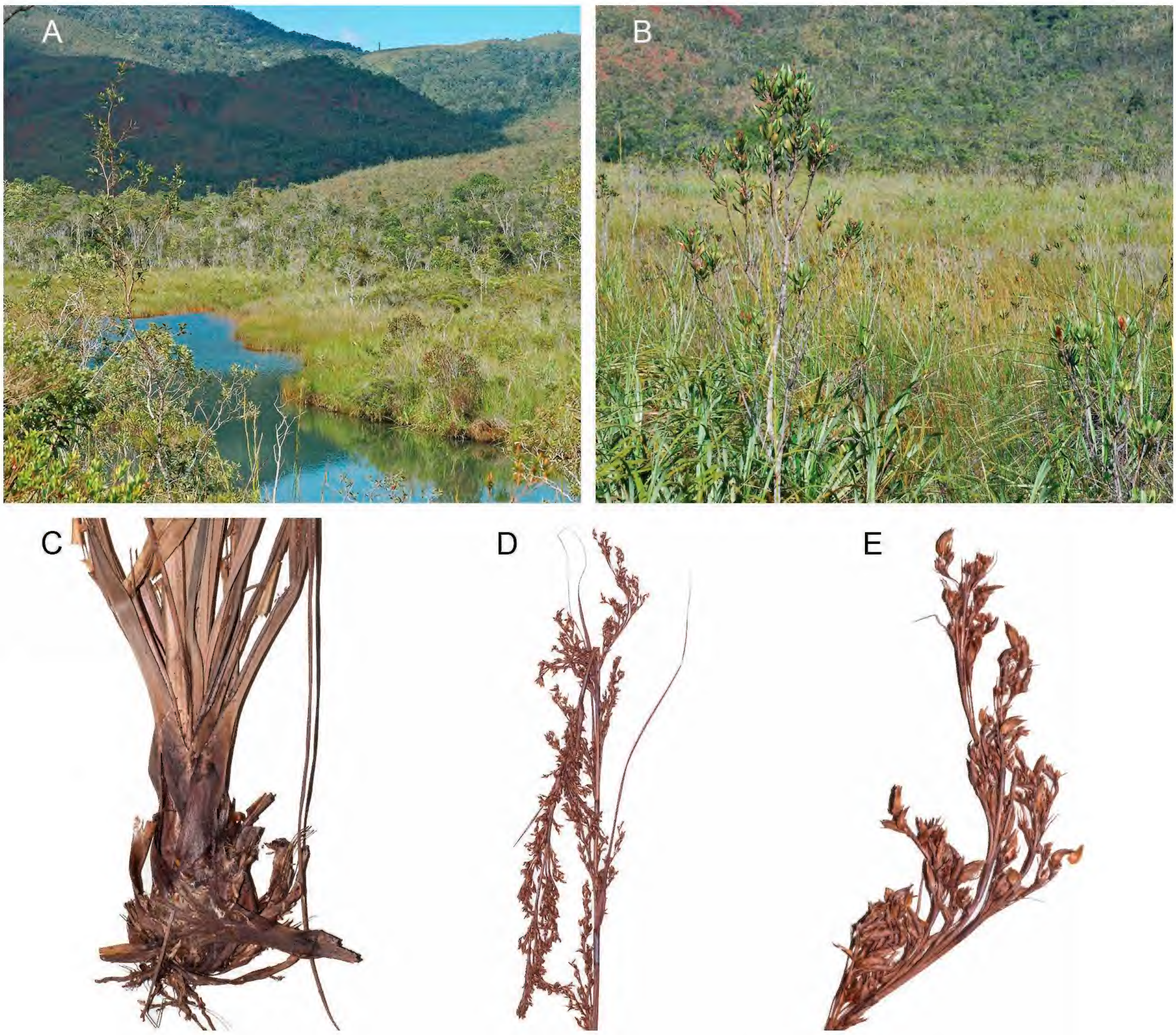

Fig. 12. *Tetraria arundinacea*. A, B. Habitat in maquis zone, Rivier Bleue, New Caledonia. C. Mature plant base. D, E. Inflorescence. C–E from *K.L. Wilson 7085* (NSW). Photos A, B by J. Munzinger; C–E by R.L. Barrett.

Diagnostic characters: Closely related to *Tetraria raynaliana* Larridon (formerly *Costularia pubescens* J.Raynal), which differs in the leaf lamina being ± flat in section (*vs* ± V-shaped); pubescent (*vs* glabrous); leaf margins ciliate (*vs* scabrous); leaf keel pilose (*vs* glabrous); and ciliate perianth segments (*vs* scabrous). *Tetraria sylvestris* (J.Raynal) Larridon (formerly *Costularia sylvestris* J.Raynal), differs in the broader leaves, 15–25 mm wide (*vs* 5–10 mm); leaves ± M-shaped in section (*vs* ± V-shaped); arcuate (*vs* ± erect) inflorescence branches and elongate persistent style base ± as long as the nutlet (*vs* ± 1/4 as long).

Distribution: Endemic to New Caledonia, widespread on the main island, Grande Terre, also on the Isle of Pines and the Bélep Islands.

Habitat: Grows most commonly in maquis, in swamps and wet slopes, but also in *Nothofagus* and *Araucaria* forests, on a variety of ultramafic soil types, commonly on serpentinite, from 50–1500 m altitude (Wulff *et al.* 2010). This species is an important component of many maquis habitat and can be dominant, particularly in disturbed areas such as rehabilitation areas and roadsides (Raynal 1974). Recorded in association with *Actinoschoenus filiformis*, *Araucaria laubenfelsii*, *A. montana*, *Babingtonia leratii*, *Bikkia macrophylla*, *Chorizandra cymbaria*, *Codia discolor*, *Cunonia lenormandii*, *Dracophyllum ramosum*, *D. verticillatum*, *Exocarpos neocaledonicus*, *Fimbristylis dichotoma*, *Gahnia microcarpa*, *G. novocaledonensis*, *Gleichenia dicarpa*, *Hibbertia emarginata*, *Lepidosperma perteres*, *Lycopodium deuterodensum*, *Machaerina deplanchei*, *M. gunnii*, *M. rubiginosa*, *Melaleuca quinquenervia*, *Meterosideros francii*, *M. nitida*, *Nothofagus* sp., *Podocarpus sylvestris*, *Polyscias pancheri*, *Scaevola balanse*, *S. beckii*, *Schoenus neocaledonicus*, *S. tendo*, *Scleria levis*, *Sphenomeris deltoidea*, *Sticherus flabellatus*, *Styphelia cymbulae*, *Symplocus montana*, *Tristaniopsis glauca* and *Wikstroemia indica*.

Phenology: Flowers mainly (April) June–December. Fruits mainly December–April.

Selected specimens and images examined: NEW CALEDONIA: Presqu'île Bogota, 28 June 1914, *R.H. Compton 1343* (BM, NSW); Les Dalmates, tributary of Ya River; road to Yatè and Parc de la Rivière Bleue, 11.3 km NE of turn-off from road to Mt Dore and Plum, 3 Nov. 2003, *D.M. Crayn et al. 755* (NSW); Mount Humboldt, 7 Nov. 1924, *A.U. Däniker 548* (Z*); Tiaré, 1861–1867, *M. Deplanche 240* (Z*); Touho: Tegan, 10 Oct. 1971, *H.S. McKee 24422* (CANB, CHR, *n.v.*, NY, P*, Z*); Pouébo: Mt Mandjela (Exploitation forestière Frouin), 12 Apr. 1972, *H.S. McKee 25211* (BISH*, G, MO, *n.v.*, NOU, *n.v.*, NSW); Touho: Ponandou, 15 June 1974, *H.S. McKee 28844* (CANB); Galarino, 22 July 1974, *H.S. McKee 28916* (NSW); Haute Tiwaka: Hauteurs de Bobetio, 29 July 1976, *H.S. McKee 31661* (NSW); Mont Nakada (Crête Nord-Est), 6 Oct. 1977, *H.S. McKee 33926* (NSW); mine des Thermopylee (6 km WNW of Thio), 1 Oct. 1971, *J. Raynal 16522* (BISH*, CANB, CHR, *n.v.*, NOU, *n.v.*, Z*); Auf den Bergen bei Yaouhé, 22 Sept. 1902, *F.R.R. Schlechter 14765* (NSW, Z*); Auf den Bergen bei Paita, 7 Oct. 1902, *F.R.R. Schlechter 14957* (NSW); Montagne des Sources, Réserve Intégrale, 19 Mar. 1987, *K.L. Wilson 7062* (AD, NSW); 7 km directly WNW of Thio on Do Thio [River], 24 Mar. 1987, *K.L. Wilson & R. Cherry 7113* (NSW); track to summit of Montagne des Sources from car-park, 4 Feb. 1991, *K.L. Wilson 7747* (NSW); Plateau de Dogny, 6 Feb. 1991, *K.L. Wilson 7770* (GENT, NSW, P); Rivière Bleue Provincial Park, 3.7 km NW of Pont Perignon on road to Pont Germain, 12 June 2001, *K.L. Wilson 9935* (NSW); Dôme de Tiébaghi, *c.* 250 m WSW of highest point, *c.* 2 km SSE of old village, 15 Aug. 2001, *K.L. Wilson 9948 & J. Stockard* (NOU, NSW, P).

Conservation: Relatively widespread and locally common, including in several reserves, so not considered threatened. IUCN: Least Concern.

Etymology: Presumably named from the similarity in form of the plant to the grass genus *Arundo* L.

Common name: None known.

Typification: No type was nominated by Hiepko (1969) who simply cited Forster material at B (*Willdenow Herbarium No. 1117*). Hiepko annotated the sheet at B as an isotype. Similarly, Hansen and Wagner (1998) cited the label details of the specimen at C but did not designate a formal status for the specimen. The protologue only matches the specimen at C (C 10010116), based on a stamp 'Hb. Vahlian.' and text 'Coll. Forst. ded. Dr. Fabri.', both absent from the other duplicates, and we therefore accept it as the holotype (Turland *et al.* 2018; Art. 9.1). Johan Christian Fabricius, who was Professor at the University of Kiel, presumbably supplied Vahl with this Forster specimen, now incorporated at C. There are duplicates of this collection at B, BM and K, each with slightly differing labels.

It is debatable whether the text 'Schoenus radiatus. *Forst. prodr. n.* 491.' should be included as indicating type material, however we conclude that only a single collection is involved in any case. We have found only one sheet actually labelled with Forster's Prodr. No. 491, at BM (BM 000991059), a fragment probably taken from the sheet at K (K 000960113).

Notes: The authorship of the name is not obvious as there are at least two options for the appropriate citation. There is no mention of Solander by Vahl (1805: 220), however indirect reference to Solander being the original author of the name is made through the inclusion of the text 'Schoenus radiatus. *Forst. prodr. n.* 491.' This is itself confusing, as No. 491 in Forster (1786: 89) is '*Schoenus arundinaceus* S. Noua Caledonia.' [S. being Solander], but that name is a *nomen nudum*. It appears that 'radiatus' is a typographic error for 'arundinaceus' in this case as Vahl treats *Schoenus radiatus* L.f. on page 260 of the same publication. While the name could be attributed solely to Vahl, we accept the indirect reference to Solander through the citation of Forster (1786) as attribution to Solander, so cite the name here as 'Sol. ex Vahl', which is in keeping with tradition for this name.

A rapid coloniser with high potential for stabilisation of erosion areas and mine site rehabilitation due to rapid and extensive root growth (Gonin *et al.* 2013; Demenois *et al.* 2017). This species is consistently colonised by arbuscular mycorrhiza (Perrier *et al.* 2006).

Däniker (1932: 76) discussed a variant of *Lophoschoenus arundinaceus*, but we include this within the variation of *Tetraria arundinacea*. Kükenthal (1939a) distinguished *Costularia daenikeri* from *C. arundinacea* based on the dilated bases of the perianth segments and the purple-black apex to the glumes. Raynal (1974) concluded that Kükenthal observed immature nutlets, and that these characteristics are not taxonomically significant.

This species is sometimes confused with *Gahnia sieberiana* Kunth due to similarities in plant habit.

Tetraria capillacea (Thunb.) C.B.Clarke, in Durand and Schinz, *Conspect. Fl. Afr.* 5: 659 (1894).

Schoenus capillaceus Thunb., *Prodr.* 16 (1794). *Chaetospora capillacea* (Thunb.) Nees, *Linnaea* 9: 299 (1834).

Type citation: None cited [but by implication from the title of the work: Cape of Good Hope, 1772–1775, *C.P. Thunberg*].

Type: South Africa: e Cap. b. spei. [1772–1775], *C.P. Thunberg s.n.* (holo: UPS (V-001320), *n.v.*; iso: B, *n.v.*, probably destroyed).

Chaetospora flexuosa var. β *gracilis* Boeckeler, *Linnaea* 38: 304 (1874).

Type citation: 'Prom. bon. spei (Bergius, Krebs, Burchell no. 566, n. 8063. B., Mundt. β. Eckl. hb. no. 112. et cum aliis plantis mixt a).'

Type: Table Mountain near Cape Town, [pre 1815], *W.J. Burchell 566* (lectotype (here designated): K 001322023*).

Residual syntypes: South Africa: 'An Fluβufern und steinigen Stellen der Küstenregion von Kapland: Kap Distr., am Tafelberg,' *Bergius s.n.* (syn: ?B, likely destroyed); Caledon Division: Nieuw Kloof, Houw Hoeck Mountains [Houhoekberge], 16 March 1815, *W.J. Burchell 8063* (syn: K 001322021*); Western Cape Division: 1 [Worcester, Waterfall], December, *C.F. Ecklon & C.L.P. Zeyher 1.12* (syn: MEL 2463578); In monte tabulari, 22 Mai 1821, *Krebs s.n.* (syn: K 001322024 (ex B)*); 'Kapland s.l.,' *Mundt* (syn: ?B, likely destroyed).

Tetraria capillacea var. *intercedens* Kük., *Repert. Spec. Nov. Regni Veg.* 29: 189 (1931).

Type citation: 'Koude Rivier (Schlechter Nr. 9739!); Genadental (Schlechter Nr. 9825!).'

Type: Koude Rivier, 243 m, 15 Dec. 1896, *F.R.R. Schlechter 9739* (lectotype (here designated): P 00461878*; isolecto: L 1399045*, P P00461877*, P P00461879*, S 13-18894*, WAG 0108310*).

Residual syntype: SOUTH AFRICA: Worcester District: Genadendal auf Bergen, 1463 m, 23 Dec. 1896, *F.R.R. Schlechter 9825* (G, *n.v.*, L 1399634*, PRE, *n.v.*, S G-6794*, WAG 1777101*, WAG 0389339*).

Chaetospora flexuosa auct. non Schrad.: Drège, *Linnaea* 20: 251 (1847), as to *Ecklon & Zeyher 4437* (P*).

Image: Vánky (2009; fig. 12, smutted).

Perennial tufted herb, 0.3–0.9 m high; plants clonal, compact, clones 0.2–0.6 m across; rhizome thick, woody, short, branched, 5–15 mm diam., non-pseudobulbous; old leaf sheaths covering the rhizome, breaking apart into fine fibres with age, reddish brown to dark brown; roots sand-binding. *Caudex* absent. *Culms* slender, rigid, erect, 30–60 cm long below inflorescence, with 1–3 nodes, terete, finely striate, 1.5–3.1 mm diam., glabrous, green, base not enlarged. *Leaves* mostly basal, numerous, and 1–3 cauline; phyllotaxy loosely spirotristichous; sheath 18–82 mm long, 1.0–1.9 mm wide, broader than the leaf lamina, margins rapidly breaking apart, glabrous, chestnut-brown, shiny, upper margin narrowly membranous, oblique to truncate, ligule absent; cauline sheath tight around culm, dark brown to black; *pseudopetiole* obscure or absent; leaves not exceeding the culms, lamina dorsiventral, 12–48(–75) cm long, 0.5–0.7 mm wide; bases not differentiated; lamina setaceous, ± linear, channelled throughout (± V-shaped in section), ± flexuous, old leaf tips not curling, finely multi-striate, lamina glabrous, green to yellow green, ± concolorous, strongly keeled along mid-nerve, margins very finely scabrous, not recurved to involute, apex long-attenuate; lowest leaves not reduced to a sheath. *Inflorescence* dense but elongate, panicle-like, narrow, ± linear, ± erect, with 4–7(–10) nodes, 6–25 cm long, 0.8–1.5 cm wide, interrupted to ± continuous, axis green to yellow-green, not glaucous; bracts reduced leaf-like at the base, bract-like with a slender lamina above, usually exceeding the branchlets, sheaths open, not enveloping the higher bracts, gradually reducing along the inflorescence, basal bract usually somewhat shorter than or equal to inflorescence, 6.5–21 cm long; basal branchlets 4.6–8.5 cm long, 1 or 2 arising in each bract axil; branches erect, each with 3–5 spikelets, spikelets solitary or appearing paired on compressed, scabrous-margined peduncles 0.5–15 mm long. *Spikelet prophyll present*, sheath 3.3–3.7 mm long, brown, midrib

distinct, partially enclosing the spikelet, with a slender lamina 0.3–0.7 mm long, brown. *Spikelets* 25–55 per inflorescence, brown, elliptic to lanceolate, 5.5–10.5 mm long, 1.5–2 mm wide, subterete, 5–9 glumes, only topmost 2(3) fertile, lower flower bisexual, functionally male, upper 1(2) bisexual, fertile, no reduced glume above the florets; glumes distichous, basal glume 2.2–2.8 mm long, fertile glumes 6.0–8.5 mm long, 0.8–1.6 mm wide, membranous, red-brown, glabrous on the keel, margins translucent and minutely ciliate, lamina glabrous to minutely scabrid, ovate, acute, with a mucro to 0.7 mm long, keel distinct only towards the apex; rachilla compact and not sinuous in fruiting spikelets. *Perianth segments* absent or 6, whitish, 0.4–0.6 mm long, *c.* one quarter as long as the nutlet, base not dilated, tapering to a fine point, margins glabrous. *Stamens* 3; anther connective 5.1–7.5 mm long, subulate; anthers yellow, 2.6–2.9 mm long, with a scaberulous apical appendage up to 1.1 mm long. *Style* trifid, base 4.8–5.6 mm long, slender and hispidulous in upper half, slender and glabrous in lower half, branches 1.9–2.5 mm long, hispidulous. *Nutlet* distinctly stipitate, constricted, obovoid to ellipsoid, obscurely trigonous, dull, pale brown, 2.1–3.5 mm long including the stipe and persistent portion of the style base, 1.0–1.5 mm diam., faces ± smooth (can appear finely papillose), glabrous, epidermal cells ± oblong to ovate, inconspicuous, with three fine white ribs, style base slightly enlarged, thick, persistent, shortly pyramidal; embryo Schoenus-type. Photosynthetic pathway not examined. *2n* = unknown. 1C = 0.29 pg (*Muasya 6467*; Bureš *et al*. 2013). (Figure 13)

Fig. 13. *Tetraria capillacea*. Cape Floristic Region, South Africa (A, C–E, G from Upper Elandspadkloof, Hawekwas Range; B, F from Table Mountain National Park). A. Habitat. B, C. Habit. D. Plant base. E. Inflorescences. F. Inflorescence with stamens. G. Infructescence. Not vouchered. Photos by T. Rebelo. All also posted on iNaturalist.org.

Diagnostic characters: Sister to *T. flexuosa* which differs in having leaves which are plano-convex near their base (*vs* strictly setaceous).

Distribution: Endemic to South Africa. Primarily close to the south coast of South Africa, from Cape Town north to the Winterhoek Mountain area and east to Grahamstown.

Habitat: Grows in fynbos, where it can be a dominant and defining species for some fynbos communities, most commonly on sands and shale or quartz-derived soils, in damp situations, from 90–1700 m altitude. Recorded in association with *Agathosma ovata*, *Brunia nodiflorum*, *Cliffortia ilicifolia*, *C. serpyllifolia*, *C. stricta*, *Colpoon compressa*, *Elegia juncea*, *Erica copiosa*, *E. formosa*, *E. glandulosa*, *E. sessiliflora*, *E. sparsa*, *E. speciosa*, *Ficinia fascicularis*, *Hypodiscus striatus*, *H. synchroolepis*, *Indigofera sulcata*, *Leucadendron eucalyptifolium*, *L. salignum*, *Metalasia gnaphalodes*, *M. muricata*, *Passerina vulgaris*, *Penaea cneorum*, *Priestleya hirsuta*, *Protea cynaroides*, *P. neriifolia*, *Pteridium aquilinum*, *Pterocelastrus tricuspidatus*, *Restio triticeus*, *Schoenus adnatus*, *S. quadrangularis*, *Simocheilus multiflorus*, *Struthiola hirsuta*, *Tetraria involucrata*, *T. secans*, *T. thermalis* and *Virgilia oroboides* (Hanekom *et al.* 1989).

Phenology: Flowers April–December.

Specimens and images examined: SOUTH AFRICA: Cape Province: George District, top of Outeniqua Pass, 3000 ft, 19 Oct. 1953, *R.H. Compton 24401* (P*); Malbrothkloof, 20 Feb. 1828, *J.F. Drège 1634 aa* (P*); Cape Province: Villiersdorp District, Silverstream, farm in Riviersonderend Mountains, 4000 ft, 14 May 1974, *P. Goldblatt 1827* (MO, *n.v.*, NSW, P*); Cape Province: George [District], 200–300 m, 12 Aug. 1933, *H. Humbert 9870* (P*); Camp Berg, 600 ft, 12 Aug. 1946, *M.R. Levyns 7916* (P*); Worcester District, Genadendal, 1500 ft, 2 Apr. 1897, *F.R.R. Schlechter 10307* (L*, NSW, P (3 sheets)*, WAG (2 sheets)*); Caledon District, Domt Neweberg, 3500 ft, 2 Feb. 1962, *H.C. Taylor 3024* (P*, PRE, *n.v.*); Stellenbosch District, Jakkalsvlei, Jonkershoek, 366 m, 7 Apr. 1964, *H.C. Taylor 5732* (PRE*).

Conservation: Relatively widespread in the southern Cape Province and not considered threatened. Conserved in numerous conservation areas including Agulhas National Park, Groenlandberg, Hottentots Holland, Kleinmond and Kogelberg Nature Reserves. IUCN: Least Concern.

Etymology: Based on the Latin *capillaris* (resembling hair), presumably in reference to the fine culms that spread out.

Common name: Ridge Tetrar.

Notes: This taxon may represent a species complex and a detailed taxonomic revision is needed to determine whether additional taxa should be recognised (G.A. Verboom, *pers. comm.*).

No type of *Schoenus capillaceus* was specifically cited by Thunberg (1794:16), but the full title of that work indicates that it is based on specimens collected by Thunberg, so it can be inferred that the type should be a Thunberg specimen. Thunberg's herbarium is in UPS (Forbes 1986) and it contains a specimen labelled as holotype (no image is available online, but it is available on microfiche).

Nees (1835: 192) cited material at B (without any details), a citation simply repeated by Kunth (1837: 325), and Boeckeler (1874: 305) only cited later collections. The specimen cited above at B was seen by Kükenthal prior to 1940, but appears to be no longer extant.

While traditionally included as a synonym of *T. capillacea*, the lectotype and all syntypes of *Chaetospora flexuosa* var. *gracilis* probably apply to *T. flexuosa* (except Bergius, but that specimen appears to have been destroyed). A lectotype has been chosen for *Chaetospora flexuosa* var. *gracilis* which represents the main concept of Boeckeler (1874) and has good material on the sheet, but original material of *T. capillacea* needs to be located, and a revision of the *T. capillacea* and *T. flexuosa* complexes should be undertaken to ensure the correct application of all names in this group. The name is here listed as a synonym following tradition, but this listing is rather notional following the selection of a lectotype.

Kükenthal (1931) appears to have included all syntypes of *Chaetospora flexuosa* var. *gracilis* Boeckeler except for *Ecklon & Zeyher 112* under his concept of *T. capillacea* var. *flexuosa* (Thunb.) Kük. Later, Kükenthal (1940) excluded *Ecklon & Zeyher 112* from his concept of *T. capillacea*, but in this publication, it also becomes apparent that he distinguishes a collection by Bergius as belonging to *T. capillacea*, while assigning another to *T. flexuosa*. Examination of specimens at MEL from the Sonder herbarium showed that at least two species were included under *Ecklon & Zeyher 112* as the number 112 actually represents a location and date (1 for Worcester, Waterfall, and 12 for December), so the same number simply indicates that they co-occurred. Kükenthal may have been looking at another collection that was confused due to the 'collection' number.

The application of *Tetraria capillacea* var. *intercedens* Kük. has not been determined in recent literature (e.g. Archer 2003), but it is here tentatively included as a synonym of *T. capillacea* pending more detailed studies in this complex. A single sheet of *Schlechter 9739* at P (P 00461878) is selected as the lectotype of *Tetraria capillacea* var. *intercedens* Kük. as it has ample material on the sheet.

Tetraria capillacea is the only known host species for the smut fungus *Moreaua capillaceae* Vánky (Vánky 2009).

Tetraria cernua (Levyns) Larridon, *S. Afr. J. Bot.* 118(1): 22 (2018).

Epischoenus cernuus Levyns, *J. S. African Bot.* 25: 80, fig. 4 (1958).

Type: South Africa: Cape Province: Somerset West Division: Steenbras Reservoir, 365 m, 1 May 1948, *M.R. Levyns 8873* (holo: BOL 139407*; iso: B 10 0166692*, BOL 139408*, K 000244899*, M 0107112*, MO 1515490*, NBG 0200373-0*, S G-6800*).

Illustrations: Levyns (1958; fig. 4); Browning and Gordon-Gray (1995; fig. 2).

Perennial tufted herb, 0.3–0.7 m high; plants clonal, forming dense tussocks 0.1–0.2 m across; rhizome thin, woody, short, branched, 1–2 mm diam., non-pseudobulbous; old leaf sheaths covering the rhizome, margins breaking apart into fine fibres with age, open almost to the base, pale brown to dark brown; roots sand-binding. *Caudex* absent. *Culms* 4–20 cm long below the inflorescence, very slender, rigid, erect to spreading, with 0 or 1 node(s), terete, finely striate, 0.5–0.9 mm diam., smooth, glabrous, green, base not enlarged. *Leaves* mostly basal, numerous, none or 1 cauline; phyllotaxy loosely spirotristichous; sheath 25–60(–92) mm long, 0.8–2.0 mm wide, ± equal to the leaf lamina when fresh, margins finely but rapidly breaking apart, glabrous, green to pale brown, dull, upper margin narrowly membranous, oblique, ligule absent; cauline sheath tight around culm, brown to reddish brown; *pseudopetiole* obscure or absent; leaves not exceeding the culms, lamina dorsiventral, 6–25 cm long, 0.8–2.0 mm wide; bases not differentiated; lamina ± linear, channelled throughout (initially almost flat to lunate, then involute and curling so appearing terete in section), ± rigid, drying, curling and becoming wiry by anthesis, then 0.3–1 mm wide, finely multi-striate, lamina glabrous, green, soon drying brown, ± concolorous, keel along mid-nerve not obvious, margins finely scabrous, apex long-attenuate; lowest leaves reduced to a sheath. *Inflorescence* open, elongate, panicle-like, with 1–4 nodes, 6–28 cm long, 1.5–8 cm wide, widely interrupted, axis green, not glaucous; bracts leaf-like at the base, progressively smaller above, greatly exceeding the branchlets, sheaths open, not enveloping the higher bracts, gradually reducing along the inflorescence, basal bract usually ± equal to or exceeding inflorescence, 6–25 cm long; basal branchlets 2.5–4 cm long, capilliform, margins glabrous, 1–4 arising in each bract axil; branches ± arcuate, each with 1 or 2 spikelets, spikelets solitary or appearing paired, ± sessile or with a short peduncle up to 2.5 mm long. *Spikelet prophyll present*, sheath 1.8–2.1 mm long, brown, midrib distinct, partially enclosing the spikelet, with a slender lamina 0.6–1.2 mm long, brown. *Spikelets* 7–12 per inflorescence, pale brown to red-brown, elliptic, 8–15 mm long, 1.1–2.0 mm wide, compressed to subterete, (8)9 glumes, only topmost 2 fertile, lower flower bisexual, functionally male, upper flower bisexual, fertile, with a slender reduced glume above the florets; glumes distichous, basal glume 2.8–3.1 mm long, fertile glumes 8.5–12 mm long, 1.1–1.5 mm wide, membranous, pale brown, glabrous on the keel, margins translucent and glabrous, lamina glabrous, lanceolate, acute to acuminate, mucro indistinct, keel distinct only towards the apex; glumes soon deciduous post fruiting; rachilla compact and not sinuous in fruiting spikelets. *Suprafloral axis* and rudimentary glume present, shorter than the ovary, often minute, axis free from the glume. *Perianth segments* not seen, probably absent or possibly minute. *Stamens* 3; anther connective 6.1–8.5 mm long, subulate; anthers yellow, *c.* 2.5 mm long, with a glabrous apical appendage up to 0.9 mm long. *Style* trifid, base 2.7–3.1 mm long, slender throughout, hispidulous towards the apex, branches 3.9–4.3 mm long, hispidulous. *Nutlet* distinctly stipitate, constricted, obloid to obovoid, obscurely trigonous, dull, pale brown, 1.8–2.9 mm long including the stipe and persistent portion of the style base, 1.2–1.4 mm diam., faces prominently tuberculate in the upper third with a ring of hairs at the base of the style, rugulose-tuberculate to almost smooth below, epidermal cells ± oblong to ovate, inconspicuous, with three fine white ribs, style base not or only slightly enlarged, not persistent; embryo not examined. *Photosynthetic pathway* inferred from anatomy to be C_3 (Bruhl & Wilson 2007; *Levyns 8873*). *2n* = unknown. (Figure 14)

Diagnostic characters: The small suprafloral axis and rudimentary bract are not known in any other species of *Tetraria*. The bright green culms, lax habit, and relatively few spikelets on long peduncles also give this species a distinctive appearance.

Distribution: Endemic to South Africa. Recorded in the Caledon, Clanwiliam, Ceres, Paarl, Stellenbosch, Tulbagh and Worcester Districts.

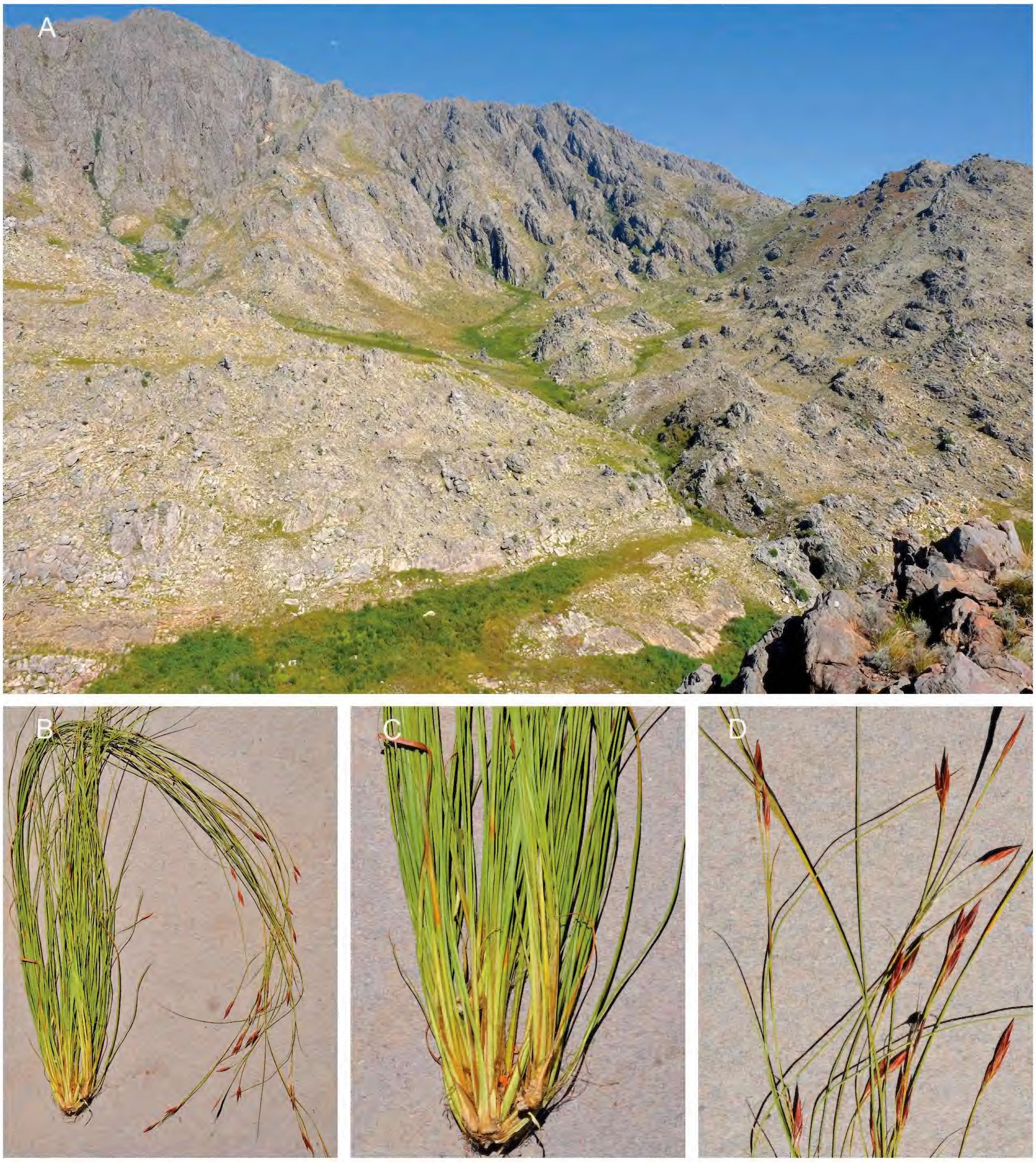

Fig. 14. *Tetraria cernua*. Visgat area, Witsenberg Mountains, Cape Floristic Region, South Africa. A. Habitat in seepage areas in valleys. B. Whole plant. C. Plant base. D. Inflorescences. From *N.A. Helme 9511* (NBG). Photos by N.A. Helme. B–D also posted on iNaturalist.org.

Habitat: Damp sandy and quartzitic soils in seasonally swampy areas that dry out over summer, from 180–1,530 m altitude. Recorded in association with *Agathosma marifolia*, *Anthospermum galioides* subsp. *galioides*, *Aspalanthus acidota*, *A. bracteata*, *Asparagus suaveolens*, *Babiana mucronata* var. *mucronata*, *Calopsis paniculata*, *Ehrharta calycina*, *Elegia capensis*, *Elytropappus adpressus*, *Eriocephalus africanus* var. *paniculatus*, *Geissorhiza confusa*, *Ischyrolepis gaudichaudiana*, *I. sieberi*, *Leucadendron salignum*, *Metalasia fastigiata*, *Paranomus bracteolaris*, *Passerina truncata* subsp. *truncata*, *Phylica oleaefolia*, *Restio perplexus*, *Romulea hirta*, *R. luteoflora*, *R. saxatilis*, *Serruria aitonii*, *S. cygnea*, *S. effusa*, *Stoebe plumosa* and *Stachys linearis* (Rebelo *et al.* 2006).

Phenology: Flowers May–November.

Specimens and images examined: SOUTH AFRICA: Clanwilliam Division: Southern Cederberg, above Krom River Kloof, 11 Dec. 1950, *E.E. Esterhuysen 17982* (BOL, *n.v.*, PRE*); Jonkersberg: Outeniqua Mountains, lower southern slopes of Engelseberg, 30 Apr. 1986, *J.H.J. Vlok 1471* (PRE, *n.v.*, WAG*).

Conservation: Somewhat restricted in distribution, with a north-south distribution of *c.* 250 km. Relatively poorly collected and in need of a detailed conservation assessment. Protected in the Cederberg and Grootwinterhoek Wilderness Areas, Groenlandberg and Haweqwa Nature Reserves, but area of extent is probably limited by relatively specific habitat requirements.

Etymology: Named from the Latin *cernuus* (inclined, stooping, nodding) in reference to the spikelets that are nodding on thin, arcuate branchlets and peduncles.

Common name: Nodding Tetrar.

Notes: The description is modified from Levyns (1958) as only specimen images and photographs of living material were examined. While included in *Epischoenus* C.B.Clarke by Levyns (1958), a possible relationship with *Tetraria* was noted at the time as it was considered somewhat intermediate between *Epischoenus* and *Tetraria*. All other *Epischoenus* species were transferred to *Schoenus* by Elliott and Muasya (2017), a relationship strongly suggested by the anatomical studies of Browning and Gordon-Gray (1995a, 1995b). The unusual morphology of *Epischoenus cernuus* was also noted by Larridon *et al.* (2018b) when they transferred this species to *Tetraria*.

Tetraria thermalis (L.) C.B.Clarke in T.Durand & Schinz, *Consp. Fl. Afr.* 5: 663 (1894).

Schoenus thermalis L., *Mant. Pl. Altera* 179 (1771). *Lepidosperma thermale* (L.) Schrad., *Gött. Gel. Anz.* 1821(3): 2070 (Tetrariae sp.), t. 4, fig. 5 (1821). *Trichoballia thermalis* (L.) C.Presl, *Symb. Bot.* 1: 9 (1830). *Sclerochaetium thermale* (L.) Nees, *Linnaea* 7(4): 512 (1832).

Type citation: '*Habitat ad aquas calidas* Capitis b. spei, *juxa montes nigros*.'

Neotype: [South Africa], Western Cape, Caledon district, Kogelberg Research Site, 7 Sep 1976, *B.J. Durand 149* (neo: PRE 0516510-0*; isoneo: NBG, *n.v.*), designated by C.Archer in S.Cafferty & C.E.Jarvis, *Taxon* 53: 180 (2004).

Sclerochaetium giganteum Steud., *Syn. Pl. Glumac.* 2(8–9): 159 (1855).

Type citation: 'Hrbr. *Drege* nr. 3965. c. sine nomine. Afr. austr.'

Type: South Africa: Cape Province: Zwischen Sparrbosch und Trado [between Sparrbosch and Trado], 1000–2000 Fuss [ft], July, *J.F. Drège 3965* (holo: P 00461932*; iso: MEL 2463532, MO 2395602*, MO 2395604*, S G-6790*).

Illustrations: Rottbøll (1773; t. 18, fig. 2); Clarke (1909; t. 91, figs 4–7); Marloth (1915: 45, t. 10 fig. A; 39, figs 5–10); Schrader (1821; t. 4, fig. 5); Schönland (1922; 61, t. 68); Metcalfe (1971; fig. 64a–d, f).

Perennial tufted, 'woody' herb, 0.9–2.5 m high; plants clonal, forming dense tussocks 0.4–2 m across; rhizome thick, woody, long, spreading, branched, 20–45 mm diam., somewhat-pseudobulbous; old leaf sheaths covering the rhizome, breaking apart into fine fibres with age only at the very base, dark brown to almost black; roots sand-binding, thick. *Culms* robust, rigid, erect, with 2–5 nodes, trigonous, finely striate, 4–8 mm diam., smooth, glabrous, green to yellow-green, base not enlarged. *Leaves* mostly basal, numerous, and 2–5 cauline; phyllotaxy loosely spirotristichous; sheath 52–80 mm long, 5–10 mm wide, narrower than the leaf lamina, margins scabrid, otherwise glabrous, dark red-brown to dark brown, dull, upper margin firm, oblique, glabrous, ligule absent; cauline sheath tight around culm; *pseudopetiole* obscure or absent; basal leaves large, but not exceeding the culms, lamina dorsiventral, 17–40(–80) cm long, 10–24 mm wide; bases brown, not dividing; lamina ± linear, ± flat to broadly V-shaped, ± flexuous, old leaf tips not curling, finely multi-striate, glabrous, green to yellow-green, strongly discolorous, weakly to strongly keeled along mid-nerve, margins scabrous, not recurved, apex long-attenuate; lowest leaves not reduced to a sheath. *Inflorescence* elongate or contracted, panicle-like, narrow, mostly erect but somewhat nodding at the apex, with (5–)6–10 nodes, 17–80 cm long, 25–50 mm wide, interrupted, axis green or yellow-green, not glaucous; bracts reduced leaf-like, just exceeding the spikelet clusters, sheaths open, not enveloping the higher bracts, gradually reducing along the inflorescence, basal bract much shorter than inflorescence, to 16 cm long; branches 1 per node, erect, with 2–6 spikelets per cluster, spikelet clusters 40–95 mm long, on short peduncles 1–3.5 mm long, fused within the base of each bract, spikelets ± sessile; 150–350 spikelets per inflorescence; lowest branch 3.5–7 cm long; spikelet prophyll present, sheath 13–16 mm long, brown, with distinct midrib, partially enclosing the spikelet, with a slender lamina 6–7.5 mm long, brown to dark brown. *Spikelets* brown to dark brown, ovate, 16–25 mm long, ± terete to greatly compressed, with 8 or 9 glumes, only topmost 3 fertile, the lower flower bisexual but functionally male, fertile, the upper 1 or 2 flowers bisexual, fertile, no reduced glume above the florets; glumes subdistichous, basal glume 12–15 mm long, fertile glumes 12–15 mm long, 2.1–3.5 mm wide, membranous, dark red-brown to dark brown, lamina glabrous below, finely puberulous in upper half, ovate-lanceolate, long-acuminate, with a mucro 5–12 mm long, keel weakly distinct, margins glabrous to minutely ciliate; rachilla

compact and not sinuous in fruiting spikelets. *Perianth segments* 6 (apparently sometimes absent), white, 3–5 mm long, not expanded below, subulate, densely covered in long, stiff hairs, almost plumose. *Stamens* 3; anther connective 12–16 mm long, subulate; anthers yellow, 3.4–3.8 mm long, with a glabrous apical appendage up to 0.7 mm long. *Style* trifid or quadrifid, base 7.5–9 mm long, glabrous at the base, but finely hispidulous for most of length, slender above, not or scarcely dilated below, branches 8–10 mm long, hispidulous. *Nutlet* prominently stipitate, stipe 3.5–4.1 mm long, constricted, ovoid to broad-ellipsoid, obscurely trigonous, dull, dark brown, 9–11 mm long including the stipe and style base, 4.1–4.5 mm diam., faces smooth, glabrous, epidermal cells irregular-oblong, inconspicuous, with three fine white ribs, style base slightly enlarged, thick, scabrous, persistent, ovoid when young, forming a small cap or shortly conical to 1.3 mm long when mature; embryo Schoenus-type. Photosynthetic pathway not examined. *2n* = unknown. 1C = 0.40 pg (*JAR02E*; Bureš *et al*. 2013). (Figure 15)

Fig. 15. *Tetraria thermalis*. Cape Floristic Region, South Africa (A, E, F from Higher Hottentots Holland, Kogelberg; B–D, G–I from Silvermine Nature Reserve, Table Mountain National Park; J from Hermanus). A–D. Habit and habitat. E. Branched caudex post-fire. F. Resprouting leaves showing ± three-ranked arrangement. G. Flowering plant. H–J. Inflorescences. Not vouchered. Photos by T. Rebelo. All also posted on iNaturalist.org.

Diagnostic characters: The large stature and spikelets distinguish *T. thermalis* from other members of the genus. Sister to *T. eximia*, which differs in being a smaller plant with more slender leaves (5–8 *vs* 10–20 mm wide) and scabrous hairs (*vs* long stiff hairs) on the perianth segments.

Distribution: Endemic to South Africa. Common in the Western Cape Province, from Cape Town east to the Mossel Bay district.

Habitat: Occurs in a range of fynbos communities, especially on sandstone derived sands. Recorded in association with *Agathosma serpyllacea*, *Aspalathus elliptica*, *A. ramulosa*, *Brunia laevis*, *Calopsis hyalina*, *C. membranacea*, *Cliffortia ferruginea*, *Cyathocoma hexandra*, *Edmondia sesamoides*, *Elegia deusta*, *E. filacea*, *E. juncea*, *E. persistens*, *E. recta*, *E. tectorum*, *Erica globiceps* subsp. *globiceps*, *E. pulchella*, *Ficinia tristachya*, *Geissorhiza hesperanthoides*, *G. hispidula*, *G. juncea*, *G. parva*, *G. schinzii*, *G. similis*, *Hypodiscus argenteus*, *Ischyrolepis capensis*, *Lanaria lanata*, *Leucadendron salignum*, *L. gandogeri*, *Mastersiella digitata*, *Metalasia brevifolia*, *M. erubescens*, *M. inversa*, *Mimetes cucullatus*, *Passerina truncata* subsp. *monticola*, *Phaenocoma prolifera*, *Protea compacta*, *P. repens*, *Restio similis*, *Retzia capensis*, *Rhodocoma fruticosa*, *Romulea dichotoma*, *R. gracillima*, *R. triflora*, *Roridula gorgonias*, *Serruria elongata*, *S. fasciflora*, *S. heterophylla*, *Stoebe aethiopica*, *Tetraria bromoides*, *T. capillacea*, *T. compar*, *T. cuspidata*, *T. fasciata*, *Thamnochortus erectus*, *T. guthrieae* and *Zyrphelis lasiocarpa* (Rebelo *et al.* 2006).

Phenology: Flowers June–October.

Specimens and images examined: SOUTH AFRICA: 56 [=Stellenbosch, Grietjesgat (=Grabouw), between Lowry's Pass and Palmiet Rivier], June, *C.F. Ecklon & C.L.P. Zeyher 111* (FI, MEL, MO*); 58.8 [=Caledon, Kleinriviersberg (=Kleinriviersberge)], Aug., *C.F. Ecklon & C.L.P. Zeyher 4439* (FI, MEL, Z*); Caledon, Aug. 1912, *F.A. Rogers 11138* (Z*); Koude Rivier, 800 ft, 15 [?July] Dec. 1896, *R. Schlechter 9731* (B, *n.v.*, NSW, Z*); Tafelberg bei Kapstadt, 24–25 Sept. 1926, *C. Schröter s.n.* (ZT-00036485*); Swellendam District, Swellendam Forest Reserve, below Eleven O'clock Peak, 610 m, 11 May 1963, *H.C. Taylor 4760* (PRE*); location, date and collector unknown (LINN HL68-16*).

Conservation: Widespread and not considered threatened. Conserved in numerous reserves including Agulhas National Park, Boosmansbos Wilderness Area, Doring River Wilderness Area, Fernkloof, Babilonstoring, Caledon, Heuningberg, Maanschynkop, Ruitersbos, Salmonsdam and Witfontein Nature Reserves. IUCN: Least Concern.

Etymology: Based on the Ancient Greek *thérmē* (heat) in reference to a mistaken belief by Linnaeus that the species grew near thermal springs (Linneaus 1771).

Common name: Bergpalmiet or Berg Palmiet.

Notes: The single sheet of *Schoenus thermalis* at LINN (HL68-16) has no details to identify the collector or year, so it cannot be established whether it is pre- or post-Linnean. While it is a possible syntype, a neotype has been designated to ensure there is no confusion over the application of this name (Cafferty and Jarvis 2004). The LINN specimen lacks leaves, which were described in detail by Linnaeus (1771), so different or additional material must have been available for description.

The nutlets are sufficiently large to be an attractive food for the Chacma Baboon (*Papio ursinus* (Kerr)), and baboons also eat the plant bases (Davidge 1978).

Despite the large inflorescences produced in this species, the equally large rhizomes have sufficient reserves to generate flowering inflorescences within two years of fire, sometimes in as little as 14 months (T. Rebelo, pers. comm.).

Tricostularia Nees ex Lehm., *Nov. Stirp. Pug.* 8: 50 (1844).

Type species: *Tricostularia compressa* Nees ex Lehm.

Discopodium Steud., *Syn. Pl. Glum.* 2(8–9): 150 (1855), *nom. illeg.*, *nom. superfl.*, *non*. Hochst. (1844).

Type species: *Discopodium drummondii* Steud.

Perennial tufted herb, 0.1–0.9(–1) m high; plants clonal, usually forming dense tussocks 0.1–0.6 m across; rhizome thin, woody, short, branched, 0.7–2.1 mm diam., non-pseudobulbous; old leaf sheaths covering the rhizome, usually not breaking apart into fine fibres with age, pale to reddish brown; roots sand-binding. *Culms* slender, rigid, erect to spreading, spirally curved in *T. aphylla*, sometimes arcuate, not or with 1–5 nodes, terete or compressed in *T. aphylla*, not or finely striate, 0.3–3.3 mm diam., smooth, glabrous, green to yellow-green, base not enlarged. *Leaves* mostly basal, numerous, and sometimes 1–5 cauline; phyllotaxy loosely spirotristichous; sheath 9–100 mm long, 0.5–3.5 mm wide, slightly broader than the leaf lamina,

glabrous except margins glabrous or scabrid, straw-coloured to dark red-brown, dull, upper margin membranous, oblique, usually finely ciliate, ligule absent; cauline sheath usually tight around culm (loose in *T. sandifordiana*); *pseudopetiole* absent, obscure or rarely distinct; basal leaves often with a much reduced lamina, not exceeding the culms, lamina dorsiventral, 0.5–12.5 cm long, 0.3–1.1 mm wide; bases white or brown-membranous, not dividing; lamina ± linear, channelled, ± flexuous, old leaf tips not curling, finely multi-striate, glabrous except for margins, green to brown, concolorous, keeled along mid-nerve or not, sometimes with 3 primary impressed nerves, margins sometimes ribbed and finely scabrous, not recurved, apex long-attenuate, setaceous; lowest leaves reduced to a sheath, lacking a lamina, pale to reddish brown. *Inflorescence* slender or contracted, panicle-like or subcapitate, straight to somewhat flexuous, not or with 1–9 nodes, 0.7–9.0 cm long, 3–17 mm wide, usually not interrupted, axis green or yellow-green, not glaucous; bracts reduced leaf-like, rarely almost pungent, not or exceeding the spikelet clusters in length, sheaths in the lower part of the inflorescence open, not or sometimes enveloping the higher bracts, gradually reducing along the inflorescence, basal bract somewhat shorter than or sometimes exceeding inflorescence, to 15 mm long; branches erect, with solitary or 2–7 spikelets, usually in a terminal cluster (rarely with a second distant cluster), spikelet(s) on short, terete, glabrous peduncles 0.2–4 mm long, arising in each bract axil; spikelet prophyll present, sheath 0.5–7 mm long, brown, with 1 or 3 distinct veins, partially enclosing the spikelet, with a slender lamina 0.6–2.5 mm long, brown. *Spikelets* brown, lanceolate to oblate, 2.8–10 mm long, terete, with 4–7(–9) glumes, only topmost 2 or 3 fertile, the lower 1 or 2 flowers male, sterile or bisexual, the upper flower bisexual, fertile, no reduced glume above the florets; glumes distichous or subdistichous, basal glume 1.4–4.5 mm long, fertile glumes 2.9–9.8 mm long, 0.7–2.8 mm wide, membranous, very pale red-brown (sometimes translucent) to very dark red-brown (apex often darker than body), often sparsely scabrous on the keel, usually ciliate on the margins, face glabrous, ovate-lanceolate, acute to acuminate or obtuse, with a mucro 0.1–1.2 mm long, keel distinct; rachilla compact and not sinuous in fruiting spikelets. *Perianth segments* 6 (rarely fewer), whitish, minute, 0.2–1.2 mm long, usually unequal, commonly expanded at base, tapering to a fine point. *Stamens* 3; anther connective 2.3–6.9 mm long, subulate; anthers yellow, pale yellow, or cream, 1.4–4.6 mm long, with a glabrous apical appendage 0.15–0.9 mm long. *Style* trifid, base 0.5–3.5 mm long, usually glabrous, sometimes hispidulous, slender above, not or scarcely dilated below, branches 1.3–3.7 mm long, hispidulous. *Nutlet* shortly stipitate, stipe 0.4–0.5 mm long, somewhat constricted, obovoid to obpyriform or broad ellipsoid, obscurely trigonous, dull, mid-brown to dark brown or almost black, 1.2–2.5 mm long including the stipe and style base, 0.8–1.5 mm diam., faces smooth, usually puberulous especially near apex, sometimes hispidulous or glabrous, epidermal cells usually square–hexagonal, inconspicuous, with three fine white ribs, style base only slightly enlarged, thick, persistent, and very shortly conical or thin and cap-like; embryo not assessed, but probably Schoenus-type. Photosynthetic pathway inferred from anatomy to be C_3 (based on three species assessed).

Diagnostic characters: Related to *Chaetospora*, differing in the non-pseudobulbous bases (*vs* not or scarcely pseudobulbous); commonly (but not exclusively) noded culms (*vs* not noded); bract-like inflorescence bracts (*vs* leaf-like); and commonly (but not exclusively) elongate inflorescences (*vs* head-like or elongate-head-like).

Distribution: Endemic to southern Australia, one species in eastern Australia, fourteen endemic to southern Western Australia. There appears to be an unusual concentration of species occurring in the Cape Riche area.

Etymology: Based on the Latin compound *tri-* (three) and *costula* (small rib), presumably in reference to the 3-ribbed fruits.

Notes: The broader definition of the genus used by authors such as Wilson (1993, 1994) and Liang *et al.* (2010) has been shown to be untenable, with several species removed to *Anthelepis* (Barrett *et al.* 2019) and we here return to the generic concept of Kükenthal (1944), but with a larger number of species recognised.

A preliminary key to species is presented here that includes four putative additional taxa that require further taxonomic study to determine their status.

Key to species of *Tricostularia*

1. Culms strongly compressed, ± flattened, 1.2–3.2 mm wide 2

1: Culms terete to compressed and oval (can be oval in *T. compressa* and *T. davisii*); 0.4–2.0 mm diam. 3

2. Culms 1.9–3.2 mm wide, strongly spirally twisted; inflorescence 4.5–9 cm long; spikelets 4.7–7.2 mm long; fertile glumes acute ..... ***T. aphylla***

2: Culms 1.2–1.9 mm wide, weakly but still distinctly twisted; inflorescence 9–13 cm long; spikelets 7–9 mm long; fertile glumes ± acuminate ..... ***T.* sp. Porongurup (I. Abbott 18)**

3. Inflorescence with 1–3 spikelets; anthers 1.4–1.6 mm long, with an apical appendage ≤0.2 mm long (eastern Australia) ..... ***T. pauciflora***

3: Inflorescence with >5 spikelets ; anthers 1.5–4.6 mm long, with apical appendage 0.3–1.2 mm long (Western Australia) 4

4. Culms not noded (or occasionally some culms with 1 node mixed with not noded culms in the same individual) below inflorescence 5

4: Culms consistently with 1–5 nodes below inflorescence 8

5. Inflorescence shortly but obviously oblong, *c.* 1.2–3.5 cm long; to about 4 times as long as wide 6

5: Inflorescence subcapitate, *c.* 0.7–1.1 cm long; to about twice as long as wide; fertile glumes pale to mid yellow-brown, acuminate 7

6. Fertile glumes pale to mid yellow-brown, acuminate ..... ***T. neesii*** (typical form)

6: Fertile glumes mid to dark red-brown, obtuse to acute ..... ***T. compressa***

7. Culms 15–35 cm tall, in ± distant clusters on linear rhizomes (Lake King region) ..... ***T. lepschii***

7: Culms 30–50 cm tall, compact on irregularly branching rhizomes (Mogumber region) ..... ***T.* sp. Mogumber (A. Harris s.n., 23/12/2015)**

8. Leaf sheaths flared strongly at the apex; culms with 2–5 nodes, distant on rhizome ..... ***T. sandifordiana***

8: Leaf sheaths not flared at the apex; culms with 1–2 nodes, close together on rhizome 9

9. Inflorescence subcapitate to obconical, *c.* 0.7–2.2 cm long 10

9: Inflorescence elongate and linear to narrow-oblong or narrow-obconical in outline, 1.5–12 cm long 12

10. Fertile glumes 3.2–4.2 mm long, with rigid cilia (0.1–0.2 mm long, regularly antrorse) near apex and on midrib; culms 0.3–0.8 mm diam. ..... ***T. davisii***

10: Fertile glumes (3.7–)4.7–5.8 mm long, with minute fine cilia (*c.* 0.05 mm long, variably antrorse to widely spreading) near apex and occasionally on midrib; culms 0.5–1.5 mm diam. 11

11. Lower (sterile) glumes 2.2–2.7 mm long; nutlet 1.2–1.5 mm long ..... ***T. bennettiana***

11: Lower (sterile) glumes 3.6–4.5 mm long; nutlet 1.9–2.2 mm long ..... ***T. neesii***

12. Inflorescence (6–)8–12 cm long; fertile glumes 6–8.8 mm long 13

12: Inflorescence 1.5–8 cm long; fertile glumes 3–5.8 mm long 14

13. Culms 1.1–2.0 mm diam.; clusters of spikelets all partly to strongly overlapping; fertile glumes 7–8.8 mm long ..... ***T. exsul***

13: Culms 0.6–1 mm diam.; clusters of spikelets distant or partly overlapping; fertile glumes *c.* 6–7 mm long ..... ***T.* sp. Two Peoples Bay (G. Wardell-Johnson GWJ 114)**

14. Inflorescence narrow-oblong or narrow-obconical, dense, with spikelet clusters ± overlapping 15

14: Inflorescence elongate and linear, with spikelets nor or scarcely overlapping 16

15. Culms 10–30 cm tall; fertile glumes 3.7–4.9(–5.6) mm long ..... ***T. bennettiana***

15: Culms (35–)45–80 cm tall; fertile glumes 4.7–5.8 mm long ..... ***T. neesii***

16: Subtending bracts shorter than or equalling spikelet clusters and therefore inconspicuous ..... ***T. newbeyi***

16. Subtending bracts at least slightly exceeding spikelet clusters and obvious 17

17. Inflorescence 3–5 cm long; fertile glumes *c.* 3 mm long ..... ***T. drummondii***

17: Inflorescence 5–8 cm long; fertile glumes *c.* 5 mm long ..... ***T.* sp. Albany (R.L. Barrett & K.L. Wilson RLB 5342)**

Tricostularia aphylla (R.Br.) K.L.Wilson & R.L.Barrett, *Austral. Syst. Bot.* 25: 286 (2012).

Lepidosperma aphyllum R.Br., *Prodr.* 235 (1810) (as '*aphylla*').

Type citation: "(M.) v.v."

Type: WESTERN AUSTRALIA: Bay I, South Coast [Lucky Bay, E of Esperance Bay], Jan. 1802, *R. Brown* [*Bennett No. 6028*] (holo: BM 000991101; iso: BM 000991102, K).

Perennial tufted herb, 0.3–0.6 m high; plants clonal, forming spreading tussocks 0.1–0.3 m across; rhizome thin, woody, short, branched, 1.6–2.1 mm diam., not pseudobulbous; old leaf sheaths covering the rhizome, not or partly breaking apart into fine fibres with age, pale brown; roots sand-binding. *Culms* stout, rigid, spreading or sometimes erect, commonly spiralling, but sometimes almost straight, with 1–2(–3) nodes strongly compressed, flat on one surface, slightly convex on the other, irregularly so towards the apex, finely striate, 1.9–3.2 mm diam., smooth, glabrous, bright light green to yellow-green, base not enlarged. *Leaves* highly reduced, 1–2(–3) cauline; phyllotaxy loosely spirotristichous; sheath 16–31 mm long, 2.1–3.4 mm wide, slightly broader than the leaf lamina, margins finely ciliate, otherwise glabrous, straw-coloured to brown, dull, upper margin firm, oblique, finely ciliate, ligule absent; cauline sheath tight around culm; *pseudopetiole* obscure or absent; basal leaves few, with only a residual lamina, much shorter than the culms, lamina dorsiventral, 0.6–1.5(–2.4) cm long, 0.7–1.1 mm wide; bases not differentiated, not dividing; lamina ± linear, ± flat to shallowly channelled, ± flexuous, old leaf tips not curling, finely multi-striate, margins very finely scabrid, otherwise glabrous, green, concolorous, slightly keeled along mid-nerve, margins not ribbed, finely scabrous, not recurved, apex long-attenuate; lowest leaves reduced to a sheath, sometimes lacking a lamina, pale brown to brown. *Inflorescence* panicle-like, narrow, linear, somewhat flexuous but ± erect, with 4–9 nodes, 4.5–9 cm long, 3–9 mm wide, usually not interrupted, axis green or yellow-green, not glaucous; bracts reduced leaf-like, not exceeding the spikelet clusters, sheaths open, not enveloping the higher bracts, gradually reducing along the inflorescence, basal bract much shorter than inflorescence, 9.5–16 mm long; branches erect, with (2–)3–7 spikelets per elongate branchlet; basal branchlet 10–26 mm long; spikelet(s) on short, irregularly-compressed, sparsely scabrous peduncles 1.5–4 mm long, arising in each bract axil; spikelet prophyll present, sheath 3.0–3.3 mm long, brown, with 3 distinct veins, partially enclosing the spikelet, with a slender lamina 0.9–2.2 mm long, brown. *Spikelets* brown, lanceolate, 4.7–7.2 mm long, 1.7–2.4 mm wide, ± terete to somewhat compressed, with (5–)7 glumes, only topmost 2 or 3 fertile, the lower 1 or 2 flowers male fertile, the upper flower bisexual, fertile, no reduced glume above the florets; glumes subdistichous, basal glume 2.7–3.1 mm long, fertile glumes 4.5–7.0 mm long, 1.5–2.2 mm wide, membranous, very pale red-brown to red-brown, lamina and keel glabrous, ovate-lanceolate, acute, not mucronate, keel weakly distinct, margins somewhat translucent and very finely ciliate; rachilla compact and not sinuous in fruiting spikelets. *Perianth segments* 6, whitish, 0.8–1.0 mm long, narrowly triangular, flattened, margins ciliate. *Stamens* 3; anther connective 5.1–6.9 mm long, subulate; anthers pale yellow, 2.0–4.0 mm long, 0.3–0.4 mm wide, with a glabrous apical appendage 0.2–0.5 mm long. *Pollen* c. triangular-pyramidal in outline, *c.* 0.025 mm long. *Style* trifid, base 1.9–2.7 mm long, hispidulous and slender above, glabrous and not or scarcely dilated below, branches 2.7–3.7 mm long, papillose-hispidulous. *Nutlet* shortly stipitate, stipe *c.* 0.5 mm long, constricted, obovoid or broad ellipsoid, obscurely trigonous, dull, mid-brown, 2.2–2.4 mm long including the stipe and style base, *c.* 1.3 mm diam., faces smooth, puberulous, most densely at the apex, with three fine white to pale yellow ribs, style base not enlarged, epidermal cells irregular, inconspicuous; embryo not examined. Photosynthetic pathway inferred from anatomy to be C_3 (*Whaite 4323A*; *Wilson 2853*; Bruhl & Wilson 2007). *2n* = unknown. (Figure 16).

Diagnostic characters: The usually spiralled, relatively broad culms are very distinctive in the genus. Spiralled culms are otherwise only found in *T.* sp. Porongurup (I. Abbott 18), which differs in having compact, sometimes subglobular inflorescences and much finer culms. Aside from the culms, it differs from *T. compressa* and *T. newbeyi* in the fewer, more distant spikelets.

Distribution: Endemic to the south-west of Western Australia, from just west of Esperance to Cape Arid, on near-coastal sand plains.

Habitat: Grows in low heath or open shrubland, usually on white sand plains, sometimes below granite outcrops, sometimes on white or yellow sand dunes, and sometimes in sandy gravel. Recorded in association with *Adenanthos cuneatus*, *A. dobsonii*, *Andersonia micrantha*, *A. parvifolia*, *Anarthria scabra*, *Aotus* sp. Esperance (P.G. Wilson 7904), *Banksia nutans*, *B. obovata, B. obtusa, B. petiolaris, B. pulchella, B. speciosa*, *Beaufortia elegans*, *Boronia crassifolia*, *Calectasia jubilaea*, *Calytrix decandra*, *Caustis dioica*, *Chaetospora curvifolia*, *C. subbarbata*, *Chordifex crispatus*, *C. sphacelatus*, *Chorizema obtusifolium*, *Conospermum distichum*, *Conothamnus aureus*, *Cyathochaeta clandestina*, *C. equitans*, *Daviesia major*, *Eucalyptus angulosa*, *E. angustissima*, *E. tumida*, *Gahnia trifida*, *Gompholobium scabrum*, *Jacksonia spinosa*, *Lepidosperma* spp., *Leptospermum spinescens*, *Logania serpyllifolia*, *Lyginia imberbis*, *Mesomelaena graciliceps*, *M. stygia*, *M. tetragona*, *Microcorys barbata*, *M. purpurea*, *Nuytsia floribunda*, *Phyllangium divergens*, *Pultenaea heterochila*, *Schoenus brachyphyllus*, *S. caespititius*, *S. cygneus*, *S. submicrostachyus*, *Stachystemon polyandrus*, *Stirlingia anethifolia*, *Stylidium breviscapum*, *S. repens*, *S. rupestre*, *Taxandria* sp., *Thelymitra granitora*, *Thomasia angustifolia* and *Trachymene pilosa*.

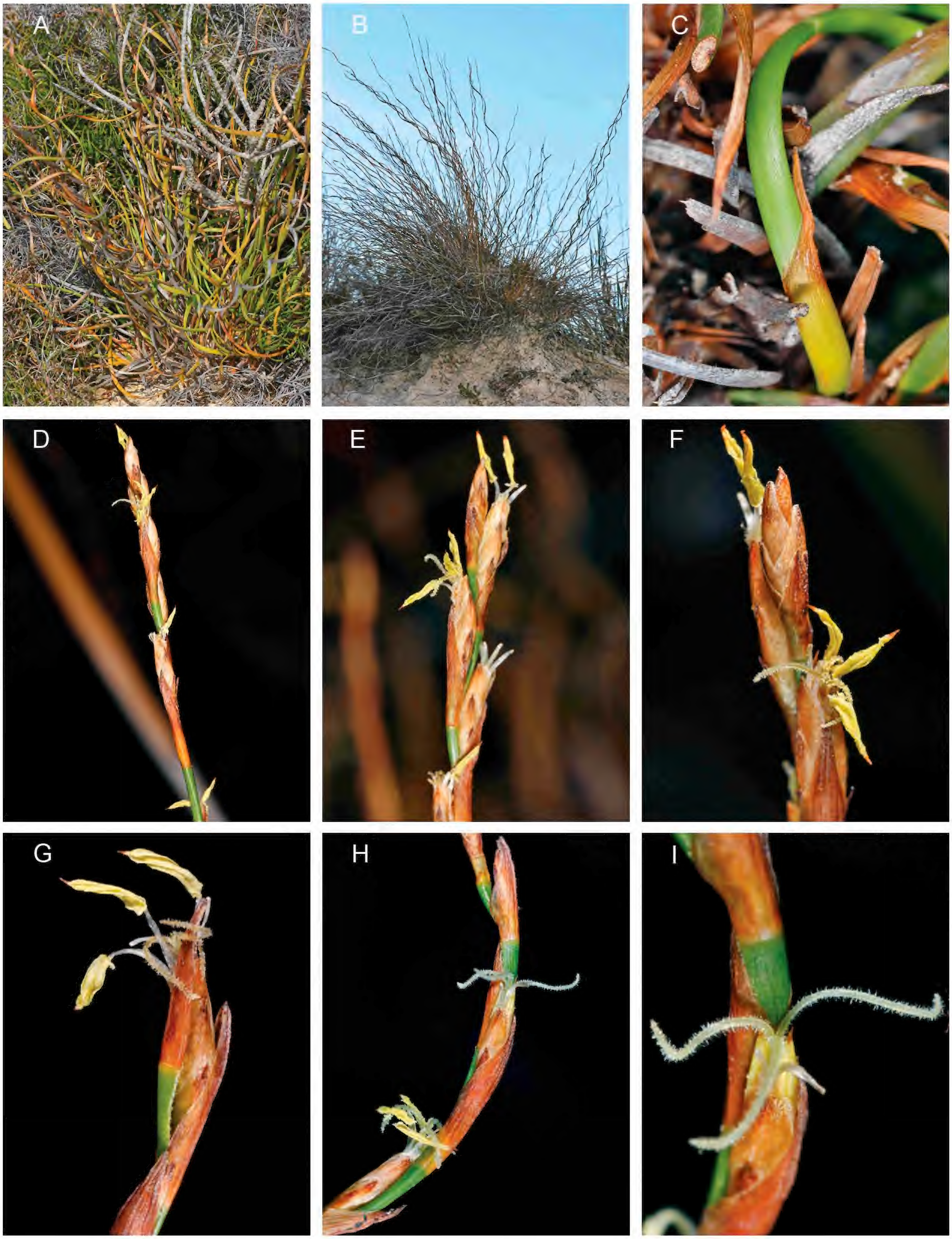

Fig. 16. *Tricostularia aphylla*. A. Habit at Lucky Bay, Western Australia. B. Habit at Cape Arid. C. Leaf sheath with reduced leaf lamina. D, E. Inflorescence. F, G. Spikelets with anthers and emerging stigmas. H, I. Spikelets with stigmas. Vouchers: A: *R.L. Barrett RLB 2753*; B: *R.L.Barrett & M.D. Barrett RLB 2905*; C–I: *R.L. Barrett RLB 4293* (all PERTH). Photos by R.L. Barrett.

Phenology: Flowers recorded for October–November. Fruit recorded for November.

Conservation status: Localised in distribution, but locally common and conserved within Cape Arid and Cape le Grand National Parks. IUCN: Least Concern.

Selected specimens examined: WESTERN AUSTRALIA: Lucky Bay Road, Cape Le Grand National Park, 14 July 2005, *R.L. Barrett RLB 2753* (PERTH); corner of Dempster Road and Scadden Road, 28 Oct. 2005, *R.L. Barrett & M.D. Barrett RLB 2905* (NSW, PERTH); cultivated material, originally collected from N side of Fisheries Road, E of Condingup Hill, E of Esperance, 18 Oct. 2007, *R.L. Barrett RLB 4293* (PERTH); *c.* 2 km S of entry to Cape Le Grand National Park, 21 Jan. 2008, *R.L. Barrett & M. Moody RLB 4307* (PERTH); Old Smokey Road, Esperance, 3 Oct. 1995, *R.J. Cranfield 10399* (NSW, PERTH); 3 km W of Israelite Bay ruins, 7 Jan. 1979, *M.D. Crisp 4884* (CBG, NSW); Esperance Bay, [1901], *L. Diels 5903* (K); Israelite Bay road, 10.7 miles E of Esperance-Norseman road, 5 Dec. 1960, *A.S. George 2003* (PERTH); 8.4 km N of Lucky Bay Road on Cape Le Grand Road, *c.* 10 km NNW of Lucky Bay, 31 Oct. 1997, *B.J. Lepschi & B.A. Fuhrer BJL 3830* (AD, CANB, MEL, NSW, PERTH); 12 km NNE of Mount Arid, Cape Arid National Park, *c.* 120 km E of Esperance, 5 Nov. 1980, *K.R. Newbey 7990* (PERTH); at Tagon Harbour, Cape Arid National Park, E of Esperance, 3 Dec. 1971, *R.D. Royce 10046* (CANB, PERTH); Esperance area, along Le Grand Road, 6 km N of border to Cape Le Grand National Park, 6 Nov. 1982, *A. Strid 21192* (K, NE, NSW, PERTH); Cape Le Grand (National Park), about 20 miles SE of Esperance, 6 Nov. 1971, *A.S. Weston 7073* (AD, CANB, PERTH); near Whartons Campsite near west end of Duke of Orleans Bay, 16 Oct. 1976, *T.M. Whaite & J. Whaite 4323A, 4323B* (K, NSW); *c.* 1 km W of Rossiter Bay on road to Lucky Bay, 14 Oct. 1979, *K.L. Wilson 2853* (NSW, PERTH); *c.* 1 km E of Whartons Campsite, Duke of Orleans Bay, 14 Oct. 1979, *K.L. Wilson 2874* (NSW, PERTH); 87 km E of Condingup on the track to Israelite Bay, Eyre District, 1 Dec. 1994, *K.L. Wilson & K. Frank KLW 9231* (NSW, PERTH); 0.5 km along Wharton Road from intersection with Orleans Bay Road, E of Esperance, 13 Oct. 2013, *K.L. Wilson 11008* (NSW); Cape Le Grand Road, 4.7 km S of Merrivale Road, 14 Oct. 2013, *K.L. Wilson 11018* (NSW); Lucky Bay, *c.* 35 km ESE of Esperance, 8 Oct. 1966, *P.G. Wilson 5599* (NSW, PERTH).

Etymology: From the Latin *aphylla* (leafless), presumably in reference to the leaves being reduced to sheaths with only a residual lamina.

Common names: Medusa Sedge; Spiral Tricostularia.

Notes: The specimen listed as holotype is from Brown's personal herbarium. The specimens listed as isotypes are known to have been separated prior to the description of the species being prepared, so they are duplicates, but were not used when preparing the description (D. Mabberley *pers. comm.*). This satisfies the criteria of Article 9.1 for recognition of a holotype (Turland *et al.* 2018).

Fertile material has rarely been collected as the spikelets are caducous once the fruit matures. In the absence of good material to determine relationships, this species was doubtfully included in *Lepidosperma* for 202 years (Barrett and Wilson 2012).

Tricostularia bennettiana R.L.Barrett & K.L.Wilson, *sp. nov.*

Type: Western Australia: 46 km E of Ravensthorpe on Esperance road, 13 Oct. 1979, *K.L. Wilson 2810* (holo: NSW 687621; iso: K, P, PERTH 2334585, READING).

Tricostularia sp. Hopetoun (M. Bennett 646), *FloraBase* (2008–), accessed 4 June 2020.

Illustration: Wheeler and Graham (2002; fig. p. 298, left-hand inflorescence only, as *T. neesii*).

Perennial tufted herb, 0.15–0.3 m high; plants clonal, forming dense tussocks 0.1–0.3 m across; rhizome thin, woody, short, branched, 1–1.5 mm diam., non-pseudobulbous; old leaf sheaths covering the rhizome, not breaking apart into fine fibres with age, pale brown; roots sand-binding. *Stems* slender, rigid, erect, with 1 node, terete, very finely striate, 0.6–1.1 mm diam., smooth, glabrous, green to yellow-green, base not enlarged. *Leaves* mostly basal, numerous, and 1 cauline; phyllotaxy loosely spirotristichous; sheath 16–28 mm long, 1.0–1.4 mm wide, slightly broader than the leaf lamina, margins very finely scabrid, otherwise glabrous, red-brown, dull, upper margin membranous, oblique, finely ciliate, ligule absent; cauline sheath tight around culm; *pseudopetiole* obscure or absent; basal leaves with a much reduced lamina, not exceeding the culms, lamina dorsiventral, 0.1–0.3 cm long, *c.* 0.05 mm wide; bases white-membranous, not dividing; lamina ± linear, ± flat, ± flexuous, old leaf tips not curling, finely multi-striate, margins very finely scabrid, otherwise glabrous when young, green, concolorous, weakly keeled along mid-nerve, margins ribbed and finely scabrous, not recurved, apex long-attenuate; lowest leaves reduced to a sheath, lacking a lamina, pale to reddish brown. *Inflorescence* contracted, panicle-like, narrow, shortly elongate, somewhat flexuous, with 2–4 nodes, 1.5–3.5 cm long, 5–8 mm wide, sometimes interrupted, axis green or yellow-green, not glaucous; bracts reduced leaf-like, with 3 distinct veins, exceeding the spikelet clusters, sheaths open, partly enveloping the higher bracts, gradually reducing along the inflorescence, basal bract much shorter than inflorescence, to 9 mm long; branches erect, with 1–3 spikelets in a terminal cluster (sometimes with a second distant cluster), spikelet(s) on short, terete, glabrous peduncles 0.5–1 mm long, arising in each bract axil; cladoprophyll subtending each spikelet bract-like, sheath 3.2–3.5 mm long, brown, with a distinct midrib, partially enclosing the spikelet, with a slender lamina

1.8–3.0 mm long, reddish brown. *Spikelets* reddish brown, lanceolate, 4–6 mm long, ± terete to somewhat compressed, with 5 or 6 glumes, only topmost 2 fertile, both bisexual, fertile, no reduced glume above the florets; glumes distichous, basal glume 2.2–2.7 mm long, fertile glumes 3.7–4.9(–5.6) mm long, 1.3–1.6 mm wide, membranous, pale red-brown to dark red-brown sparsely scabrous on the keel and margins, lamina glabrous, ovate-lanceolate, acuminate, with a mucro to 0.7 mm long, keel distinct; rachilla shortly elongate and not or scarcely sinuous in fruiting spikelets. *Perianth segments* 6, whitish, minute, 0.6–1.0 mm long, expanded below, filiform above, with a few stiff apical hairs. *Stamens* 3; anther connective 3.4–4.3 mm long, subulate; anthers cream, 2.6–3.0 mm long, with a glabrous apical appendage up to 0.5 mm long. *Style* trifid, base 3.1–4.3 mm long, glabrous and slender below, hairy and dilated in apical third, branches 2.1–2.8 mm long, hispidulous. *Nutlet* shortly stipitate, stipe *c*. 0.3 mm long, very constricted, obovoid to obpyriform, obscurely trigonous, dull, mid-brown to dark brown, 1.2–1.5 mm long including the stipe and style base, 0.8–0.9 mm diam., faces smooth, puberulous especially near apex, epidermal cells square–hexagonal, inconspicuous, with three fine white ribs, style base only slightly enlarged, thick, persistent, very shortly conical, *c*. 0.2 mm long; embryo not examined. Photosynthetic pathway inferred from anatomy to be C_3 (Takeda *et al*. 1985; *Orchard 1531*). *2n* = unknown. (Figure 17).

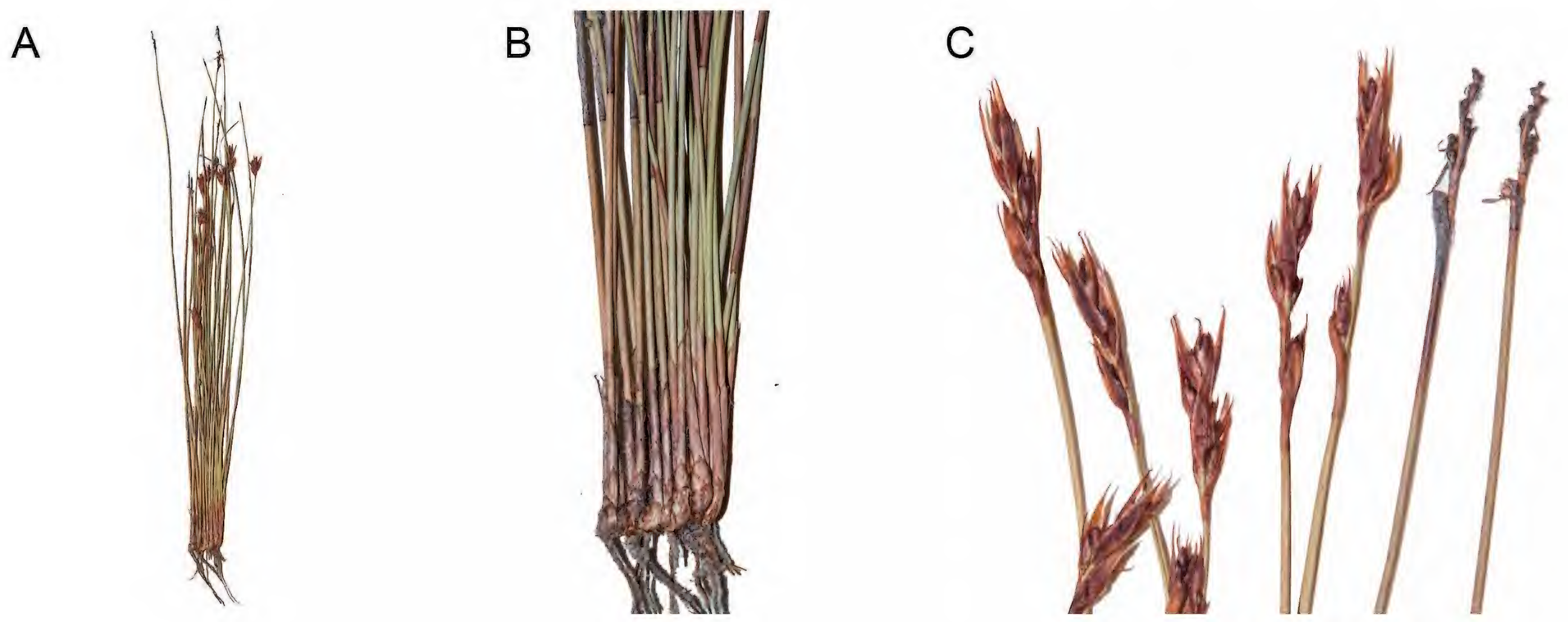

Fig. 17. *Tricostularia bennettiana*. A. Habit at Stokes Inlet, Western Australia. B. Plant base with sand-binding roots. C. Inflorescences (including old inflorescence axes on right hand side). Vouchers: A, B: *A.E. Orchard 1531* (NSW); C: *K.L. Wilson 2932* (NSW). Photos A–C by R.L. Barrett.

Diagnostic characters: Related to *T. neesii*, differing in the tightly tufting habit, thin, culms with one node, shortly elongate, robust, inflorescences and inflorescence bracts exceeding the paired spikelets.

Distribution: Endemic to the south-west of Western Australia, between Ongerup and Cape Arid.

Habitat: Grows in deep white, yellow or grey sands on plains, sometimes adjacent to salt pans, or on gentle slopes, growing in heath or open mallee scrub. Recorded in association with *Banksia gardneri*, *Caustis dioica*, *Cyathochaeta clandestina*, *Eucalyptus tetragona*, *E. tetraptera*, *Lepidosperma carphoides*, *L.* sp. Clathrate (R.L. Barrett & G.F. Craig RLB 3570), *L.* sp. Jerdacuttup (R.L. Barrett RLB 2770), *L.* sp. P2 Capitate (K.L. Wilson 2798), *L.* sp. Z dark sheath (P.G. Wilson 10177), *Mesomelaena stygia*, *Schoenus caespititius*, *S. cygneus*, *S. submicrostachyus* and *Tricostularia lepschii*.

Phenology: Flowers October–November.

Conservation status: Recorded as locally common and probably not threatened. Conserved within Fitzgerald River National Park. IUCN: Least Concern.

Specimens examined: WESTERN AUSTRALIA: Hopetoun airstrip, turnoff on road 5.8 km N of Hopetoun, 21 Oct. 2000, *M. Bennett 646* (PERTH); 0.2 km E of Rock Hole Road on Rawlinson Road, Reserve 31754, Oct. 1984, *M.A. Burgman 4572* (PERTH); 17 miles from Ravensthorpe, towards Lake King (315–316 mile posts), 6 Nov. 1968, *E.M. Canning 7256* (NSW, PERTH); NE of Jerramungup, 20 Nov. 1965, *A.S. George 7038* (PERTH); Boxwood Hill, at junction of South Coast Highway and Bremer Bay Road, 8 October 2003, *J. Hodgon 813 & J.J. Bruhl* (BOL, EIU, GENT, K, MO, NE, NSW, NY, PERTH, PRE); scrub N of Fisheries Road, *c*. 10 km ESE of Howick Hill, Eucla Division, Esperance district, 17 Sept. 1968, *E.N.S. Jackson 417* (PERTH); 30 km SE of Ongerup, 5 Nov. 1974, *K.R. Newbey 4915* (PERTH); near western border of Shire of Esperance, Location 1099, *c*. 45 km N of the coast at Stokes Inlet, Eucla Division, 14 Oct. 1968, *A.E. Orchard 1531* (AD, *n.v.*, CANB,

NSW, PERTH); below Perkins Rock, Fitzgerald River Reserve [National Park], 22 Oct. 1970, *R.D. Royce 9216* (PERTH); 19 km S of Lake King on Ravensthorpe road, 13 Oct. 1979, *K.L. Wilson 2803* (NSW, P, PERTH); S of Lake King, 6 Nov. 1994, *K.L. Wilson 8780* (NE, NSW, PERTH); opposite Jerdacuttup wheat silo, 6.7 km S of South Coast Highway on Fence Road, 29 Nov. 1994, *K.L. Wilson 9163* (NE, NSW, PERTH).

Etymology: Named in honour of botanist Merle Bennett OAM (1929–), of Hopetoun, long-time coordinator of the Ravensthorpe Wildflower Show and Ravensthorpe Regional Herbarium. She has contributed many valuable plant specimens to the Western Australian Herbarium, including this species. She is a co-author of *Native plants of the Ravensthorpe region* (Craig *et al.* 2011).

Common name: Bennett's Tricostularia.

Notes: A relatively distinctive species that was previously confused with immature specimens of *T. compressa*.

Tricostularia compressa Nees ex Lehm., *Nov. Stirp. Pug.* 8: 51 (1844).

Chaetospora spicata Boeckeler, *Linnaea* 38(3): 297 (1874), *non Chaetospora compressa* Gray (1821). *Schoenus tricostularia* F.Muell., *Syst. Census Austral. Pl.* 1: 128 (1882).

Type citation: "Crescit in locis rupestribus collium "Konkoberup Hills" (Kent) (Herb. Preiss no. 1800.)"

Type: Western Australia: Konkoberup Hills, Kent [= Mount Melville, near Cape Riche], 21 Nov. 1840, *L. Preiss* [*Pl. Preissianae No. 1800*] (lectotype (here designated): LD 1732307; isolectotypes: G 00195293, MEL 2297587, MEL 2297588, P 01926657).

Illustration: Kaphahn (1905; figs 19, 20).

Perennial tufted herb, (0.15–)0.3–0.45 m high; plants clonal, forming dense to spreading tussocks 0.1–0.6 m across; rhizome thin, woody, short, branched, 0.7–1.2 mm diam., not pseudobulbous; old leaf sheaths covering the rhizome, not breaking apart into fine fibres with age, pale brown, prominently nerved; roots sand-binding. *Culms* slender, rigid, erect, not noded or occasionally with one node just below the inflorescence, compressed, semi-terete or terete, not or finely grooved, 0.4–0.6 mm diam., smooth, glabrous, dull green to yellow-green, base not enlarged. *Leaves* all basal, 2 or 3; phyllotaxy loosely spirotristichous; sheath 9–44 mm long, 0.8–0.9 mm wide, much broader than the leaf lamina, margins glabrous, reddish-brown at the base, straw-coloured or pale brown above, dull, upper margin narrowly membranous, oblique, glabrous, ligule absent; sheath tight around culm; *pseudopetiole* obscure or absent; leaves usually with a much reduced lamina to 1 mm long, to 0.3 mm wide, but young or regenerating plants sometimes have a lamina to 11 cm long; lamina highly reduced, ± triangular, glabrous, brown, concolorous, apex acute. *Inflorescence* contracted, panicle-like, narrow, erect, with 2–4 nodes, 1.5–3.2 cm long, 4–7 mm wide, usually somewhat interrupted, axis green or yellow-green, not glaucous, a few short, scabrid hairs on the margins; bracts reduced, not exceeding the spikelet clusters, light or orange-brown, shiny, sheaths open, not enveloping the higher bracts, gradually reducing along the inflorescence, basal bract much shorter than inflorescence, 7–11 mm long; branches erect, with 3–5 spikelets per cluster, arising in each bract axil, spikelet on short, compressed, glabrous peduncles *c.* 1 mm long; spikelet prophyll present, sheath 1.3–1.5 mm long, brown, with distinct midrib, partially enclosing the spikelet, acuminate, with a slender lamina 0.4–0.9 mm long, brown. *Spikelets* brown, ± oblate, 2.8–5.1 mm long, 0.9–1.6 mm wide, compressed, with 4 or 5 glumes, only topmost 2 fertile, the lower flower male, fertile, the upper flower bisexual, fertile, no reduced glume above the florets; glumes subdistichous, basal glume 1.4–2.3 mm long, fertile glumes 3.3–4.1 mm long, 0.8–1.1 mm wide, membranous, pale brown, orange-brown or red-brown (apex often darker than body), keel and lamina glabrous, ovate, obtuse to acute, mucro absent, keel distinct; rachilla compact and not or scarcely sinuous in fruiting spikelets. *Perianth segments* 6, whitish, minute, 0.3–0.9 mm long, subulate, tapering to a fine point. *Stamens* 3; anther connective 3.0–3.7 mm long, subulate; anthers pale yellow, 2.8–3.5 mm long, with a glabrous apical appendage up to 0.5 mm long. *Style* trifid, base 1.4–1.7 mm long, glabrous, slender, slightly tapering below, branches 1.3–1.9 mm long, hispidulous. *Nutlet* shortly stipitate, stipe *c.* 0.5 mm long, somewhat constricted, ± obovoid, obscurely trigonous, dull, mid-brown, 1.6–1.8 mm long including the stipe, 0.9–1.0 mm diam., faces smooth but shortly hispidulous, epidermal cells ovoid–hexagonal, inconspicuous, with three fine, hispidulous white ribs, style base not enlarged; embryo not examined. Photosynthetic pathway not examined. (Figure 18).

Diagnostic characters: Rhizome very compact. Culms compressed to terete, usually nodeless. Inflorescence short, compact (1.5–3.2 cm long). Inflorescence bracts short, lower bract 7–11 mm long, not exceeding lower branchlet.

Distribution: Endemic to the south-west of Western Australia, between Walpole, the Stirling Range and Cape Arid.

Fig. 18. *Tricostularia compressa*. A–C. Flowering inflorescences at Bayonet Head. D–F. Immature or depauperate inflorescences. G. Habit at Stirling Range, Western Australia. H. Plant base. I. Inflorescence. Vouchers: A–C: *G. Byrne 4483* (PERTH); D–F; *G. Byrne 4941* (PERTH); G, H: *A. Strid 21578* (NSW); I: *J.H. Maiden s.n.* (NSW 75058) Photos A–F by G. Byrne; G–I by R.L. Barrett.

Habitat: Grows in Proteaceae dominated shrublands and heath and mallee woodlands in deep to shallow white or grey sands or clay soils, commonly with gravel or laterite, sometimes over granite, in red-brown sandy loam or pale grey loamy sand, on flat or undulating sandplains, old sand dunes and gentle slopes. Recorded in association with *Acacia* sp., *Adenanthos apiculatus*, *A. drummondii*, *Allocasuarina humilis*, *Anarthria humilis*, *Austrostipa* sp., *Banksia coccinea*, *B. falcata*, *B. nutans*, *B. obovata*, *B. plumosa*, *B. prostrata*, *Boronia spathulata*, *B. speciosa*, *Caustis dioica*, *Chaetanthus tenellus*, *Chordifex capillaceus*, *Chorizandra enodis*, *Conospermum*

coerulescens, *C. floribundum*, *Conostylis vaginata*, *Desmocladus fasciculatus*, *D. laxiflorus*, *Eucalyptus angulosa*, *E. marginata*, *E. pachyloma*, *E. pleurocarpa*, *Gahnia trifida*, *Gastrolobium retusum*, *Gompholobium villosum*, *Goodenia trinervis*, *Grevillea cagiana*, *G. nudiflora*, *Hakea ceratophylla*, *H. corymbosa*, *H. cucullata*, *H. denticulata*, *H. ferruginea*, *H. florida*, *H. laurina*, *H. marginata*, *H. nitida*, *H. pandanicarpa* subsp. *crassifolia*, *H. trifurcata*, *Lambertia inermis*, *Lepidosperma* spp., *Leucopogon tamariscinus*, *Machaerina juncea*, *Melaleuca suberosa*, *M. thymoides*, *M. violacea*, *Mesomelaena stygia*, *M. tetragona*, *Nuytsia floribunda Oligarrhena micrantha*, *Petrophile filifolia*, *Platytheca galioides*, *Pultenaea ericifolia*, *Regelia* sp., *Rhytidosperma* sp., *Rinzia schollerifolia*, *Schoenus brachyphyllus*, *S. globifer*, *S. subfascicularis*, *Spyridium majoranifolium Stirlingia latifolia*, *Taxandria spathulata*, *Tetratheca pubescens*, *Tricostularia exsul* and *T. neesii*.

Phenology: Flowers mainly October–December.

Conservation status: Relatively widespread and not considered threatened. Conserved in Cape Arid, Cape le Grand, Fitzgerald River and Stirling Range National Parks. IUCN: Least Concern.

Selected specimens examined: WESTERN AUSTRALIA: Bell Track N, Fitzgerald River National Park, 5 Oct. 1996, *S. Barrett 760* (PERTH); South Stirling, just W of township, 4 Oct. 1976, *B.G. Briggs 6585* (NSW); South Stirling, just W of township, 4 Oct. 1976, *B.G. Briggs 6587* (NSW); South Stirling, just W of township, 4 Oct. 1976, *B.G. Briggs 6600* (NSW, PERTH); South Stirling, just W of township, 4 Oct. 1976, *B.G. Briggs 6604* (NSW, PERTH); Reserve NW of Lower King Road, Bayonet Head, 12 Nov. 2012, *G. Byrne 4483* (NSW, PERTH); 4.3 km from the Cape Riche Camping Ground on Sandalwood Road, 27 Oct. 2013, *G. Byrne 4941* (PERTH); Cranbrook catchment, 2 km E of Cranbrook, 10 Dec. 1996, *R. Davis 1721* (PERTH); 50 m along Warramurrup Road from junction of Borden/Bremer Bay Road, c. 20 km W of Bremer Bay, 14 Nov. 2001, *R. Davis 10147* (AD, *n.v.*, PERTH); near Esperance, [1901], *L. Diels 5422* (PERTH); Eucla division, Esperance district, roadside *c.* 2 km S of Gibson, 20 Oct. 1968, *N.N. Donner 3081* (AD, NSW, PERTH); Swan River Colony, 1848, *J. Drummond 348* (MEL, P (2 sheets), PERTH); Whoogarup Range, SSW of Ravensthorpe, 2 Dec. 1960, *A.S. George 1917* (PERTH); first firebreak S of Hamilla Road, *c.* 1.2 km W of NE corner, 30 Jan. 2001, *M. Hislop 2537* (NSW, PERTH); SW of Boxwood Hill, 300 m W of South Coast Highway along Old Boundary Road, 8 Oct. 2003, *J. Hodgon 812 & J.J. Bruhl* (NE, NSW, PERTH); 7 km along Salt River Road from Formby South Road, to Cranbrook, Stirling Ranges, 14 Nov. 1982, *G.J. Keighery 5760* (NSW, PERTH); Mount Baring, Cape Arid National Park, 29 Oct. 1990, *G.J. Keighery 11791* (PERTH); on S side of Brockway Road, 4 km W of Esperance-Norseman Road. Helms Arboretum, *c.* 19 km NNW of Esperance. [Plot - ES02], 12 Oct. 2000, *G.J. Keighery & N. Gibson 5284* (CANB, NSW, PERTH); 7.1 km E of South Coast Highway on Swamp Road, *c.* 18 km N of Beaufort Inlet, 26 Oct. 1997, *B.J. Lepschi & B.A. Fuhrer BJL 3712* (AD, CANB, NSW, PERTH); 38.9 km N of Ravensthorpe on the road to Munglinup, 29 Oct. 1997, *B.J. Lepschi & B.A. Fuhrer BJL 3795* (CANB, NSW, PERTH); Kalgan Plains, Dec. 1909, *J. Maiden s.n.* (NSW 750058, PERTH 2334240); 15 km S of Needilup, 21 Oct. 1975, *K.R. Newbey 4880* (CBG, MEL, PERTH); 0.6 km N of Gibson, 26 km N of Esperance, 13 Nov. 1980, *K.R. Newbey 8170* (CBG, PERTH); *c.* 3 km N of Mount Frankland, N from Walpole on the road to Lake Muir, 11 Dec. 1974, *R. Pullen 9958* (CANB, NSW, PERTH); along Balladonia road S of Mount Ragged, Cape Arid National Park, E of Esperance, 4 Dec. 1971, *R.D. Royce 10074* (PERTH); Stirling Range National Park, southern plains W of Chester Pass Road, 11 Nov. 2004, *E.M. Sandiford EMS 988* (PERTH); At intersection of South Coast Highway and Bremer Bay Road, 22 Oct. 1982, *A. Strid 20914* (NSW); 22 km from Condingup along road to Esperance, 8 Nov. 1982, *A. Strid 21257* (NSW); Stirling Range Drive N of Toolbrunup Peak, Stirling Range National Park, 25 Nov. 1982, *A. Strid 21578* (NSW); Helms Arboretum, Brockway Road, roadside next to Eucalypt plantation, 28 Oct. 1998, *C.D. Turley 8/1098* (PERTH); 643 Boxwood Hill–Ongerup Road, Middle Track, 1.3 km W of paddock, Boxwood Hill, 19 Nov. 2007, *J.E. Wajon 1608* (PERTH); Stirling District, *c.* 20 km W of Ongerup, 11 Nov. 1974, *D.J.E. Whibley 5276* (AD, PERTH); *c.* 1 km E of Whartons Campsite, Duke of Orleans Bay, 14 Oct. 1979, *K.L. Wilson 2873* (NSW, PERTH, P); 16 km W of 'Gairdner River' on Ongerup road, 16 Oct. 1979, *K.L. Wilson 2908* (NSW, PERTH); *c.* 5 km NW of Cape Riche on Wellstead road, 16 Oct. 1979, *K.L. Wilson 2938* (NSW, PERTH, P); 1 km N of Starvation Boat Harbour on road to Springhole Road, 29 Nov. 1994, *K.L. Wilson 9174 & K. Frank* (NE, NSW, PERTH).

Etymology: From the Latin *compressus*, apparently in reference to the distinctly compressed culms (and in contrast to the terete culms of *T. neesii*).

Common name: Clustered Tricostularia.

Notes: This name has been very widely applied to a number of the taxa recognised as distinct species in this paper.

While there is only a single collection nominated as the type, sets were distributed by Nees, and the specific location of the type is not designated by Lehmann (1844). We have chosen the sheet at LD as lectotype as this was Nees' primary set and it has ample material on the sheet.

Young, resprouting or depauperate plants can have a distinctive appearance, with distinctly developed leaf laminas, somewhat flexuous to sinuous nodeless culms that are compressed and oval or sometimes angular, and small inflorescences with few spikelets. *Pullen 9958* (CANB, NSW, PERTH) has culms with 2 nodes and may be closer to *T. newbeyi*.

Tricostularia davisii R.L.Barrett & K.L.Wilson, *sp. nov*.

Type: Western Australia: 6 km SSW of Wellstead, 2 Nov. 1995, *R. Davis 302* (holo: PERTH 04423186).

Tricostularia sp. Wellstead (R. Davis 302), *FloraBase* (2008–), accessed 4 June 2020.

Perennial tufted herb, 0.1–0.6 m high; plants clonal, forming dense tussocks 0.15–0.7 m across; rhizome thin, woody, short, branched, 0.8–1.2 mm diam., non-pseudobulbous; old leaf sheaths covering the rhizome, not breaking apart into fine fibres with age, pale brown; roots sand-binding. *Culms* slender, rigid, erect, with 2 nodes, ± terete but very finely and irregularly ridged when dry, 0.35–0.8 mm diam., smooth, glabrous, green to yellow-green. *Leaves* mostly basal, few, and 2 cauline; phyllotaxy loosely spirotristichous; sheath 13–25 mm long, 0.5–0.8 mm wide, broader than the leaf lamina, margins very finely scabrid, otherwise glabrous, straw-coloured to brown, dull, upper margin narrowly membranous, oblique, finely ciliate, ligule absent; cauline sheath tight around culm for most of length, but open at the orifice; *pseudopetiole* obscure or absent; basal leaves with a much reduced lamina, not exceeding the culms, lamina dorsiventral, 0.3–1.0 cm long, 0.1–0.3 mm wide; bases not membranous, not dividing; lamina ± linear, ± flat, flexuous, finely multi-striate, margins and keel finely scabrid, otherwise glabrous, brown, concolorous, weakly keeled along mid-nerve, margins not recurved, apex long-attenuate, setaceous; lowest leaves reduced to a sheath, lacking a lamina, pale brown. *Inflorescence* subcapitate, much-contracted, panicle-like, obconic to obovate, with 3–5 nodes (but very compact and all nodes obscured by bracts), 0.7–1.5 cm long, 3–5 mm wide, not interrupted, axis green or yellow-green, not glaucous; bracts not leaf-like, long-attenuate (sometimes almost pungent), shortly to greatly exceeding the spikelet clusters, sheaths open, overlapping but not enveloping the higher bracts, gradually reducing along the inflorescence, basal bract exceeding inflorescence, to 15 mm long; branches erect, 0.5–1.1 cm long, with 1 or 2 spikelets in a terminal cluster, spikelet(s) on short, terete, glabrous peduncles 0.2–0.8 mm long, arising in each bract axil; spikelet prophyll present, sheath 0.6–0.9 mm long, brown, not enclosing the spikelet, acuminate, lamina ± absent. *Spikelets* brown, lanceolate, 3.7–5.1 mm long, 0.9–0.1.1 mm wide, semi-terete to compressed, with 6 glumes, only topmost 2 fertile, the lower flower male, the upper flower bisexual, fertile, no reduced glume above the florets; glumes distichous, basal glume 2.9–4.2 mm long, fertile glumes 3.2–4.2 mm long, 0.7–0.9 mm wide, membranous, very pale red-brown (apex often darker than body), ciliate on the keel and margins, lamina glabrous, lanceolate to obovate, acuminate, with a mucro 0.2–0.6 mm long, keel distinct; rachilla compact and not or scarcely sinuous in fruiting spikelets. *Perianth segments* 6, whitish, minute, 0.4–0.6 mm long, expanded only at base, tapering to a fine point, glabrous or apex minutely hispid. *Stamens* 3; anther connective 3.3–4.6 mm long, subulate; anthers cream, 2.4–2.6 mm long, with a glabrous apical appendage 0.6–0.8 mm long. *Style* trifid, base 1.2–2.0 mm long, glabrous, slender above, not dilated below, branches 1.4–1.9 mm long, hispidulous. *Nutlet* shortly stipitate, stipe *c.* 0.5 mm long, somewhat constricted, obovoid to obpyriform or broad ellipsoid, obscurely trigonous, shiny, dark brown to almost black, 1.2–1.7 mm long including the stipe and style base, 0.8–1.0 mm diam., faces smooth, sparsely puberulous, epidermal cells square–hexagonal, inconspicuous, with three fine white ribs, style base not enlarged, cap-like; embryo not examined. Photosynthetic pathway not examined. (Figure 19).

Diagnostic characters: Related to *T. neesii*, differing in the tightly tufting habit, thin, one or two nodes culms and small, subcapitate inflorescences with inflorescence bracts exceeding the spikelets. The erect cilia on the glume margins are also distinctive, the hairs on *T. neesii* are shorter and not erect.

Distribution: Endemic to the south-west of Western Australia, between Manypeaks and Cape Riche, east to Ravensthorpe and north to Lake King; possibly also near Witchcliffe and Beenup.

Habitat: Grows in mallee woodland and heath on flats, hillsides and valleys in a variety of soils including grey sand, brown sandy clay, swampy, peaty sand over clay, lateritic loam, granite, spongelite and soapstone, often in damp or winter-wet sites. Recorded in association with *Acacia aemula*, subsp. *muricata*, *A. luteola*, *Adenanthos cuneatus*, *Astartea aspera*, *A. pulchella*, *Calectasia gracilis*, *Chordifex capillaceus*, *Daviesia latifolia*, *Drosera roseana*, *Eucalyptus angulosa*, *E. lehmannii*, *E. neutra*, *E. preissiana*, *E. redunca*, *Franklandia fucifolia*, *Gahnia aristata*, *G. trifida*, *Gastrolobium bracteolosum*, *G. congestum*, *Goodenia incana*, *Lepidosperma carphoides*, *L. striatum*, *Leucopogon penicillatus*, *Machaerina juncea*, *Melaleuca spathulata*, *Mesomelaena graciliceps*, *M. stygia*, *Myoporum tetrandrum*, *Petrophile teretifolia*, *Pimelea angustifolia*, *Schoenus laevigatus*, *S. pleiostemoneus*, *S. subfascicularis*, *Stylidium albomontis*, *S. caricifolium*, *S. repens*, *Tricostularia compressa*, *T. newbeyi* and *Xanthosia huegelii*.

Phenology: Flowers recorded for October–November. Fruit recorded for November.

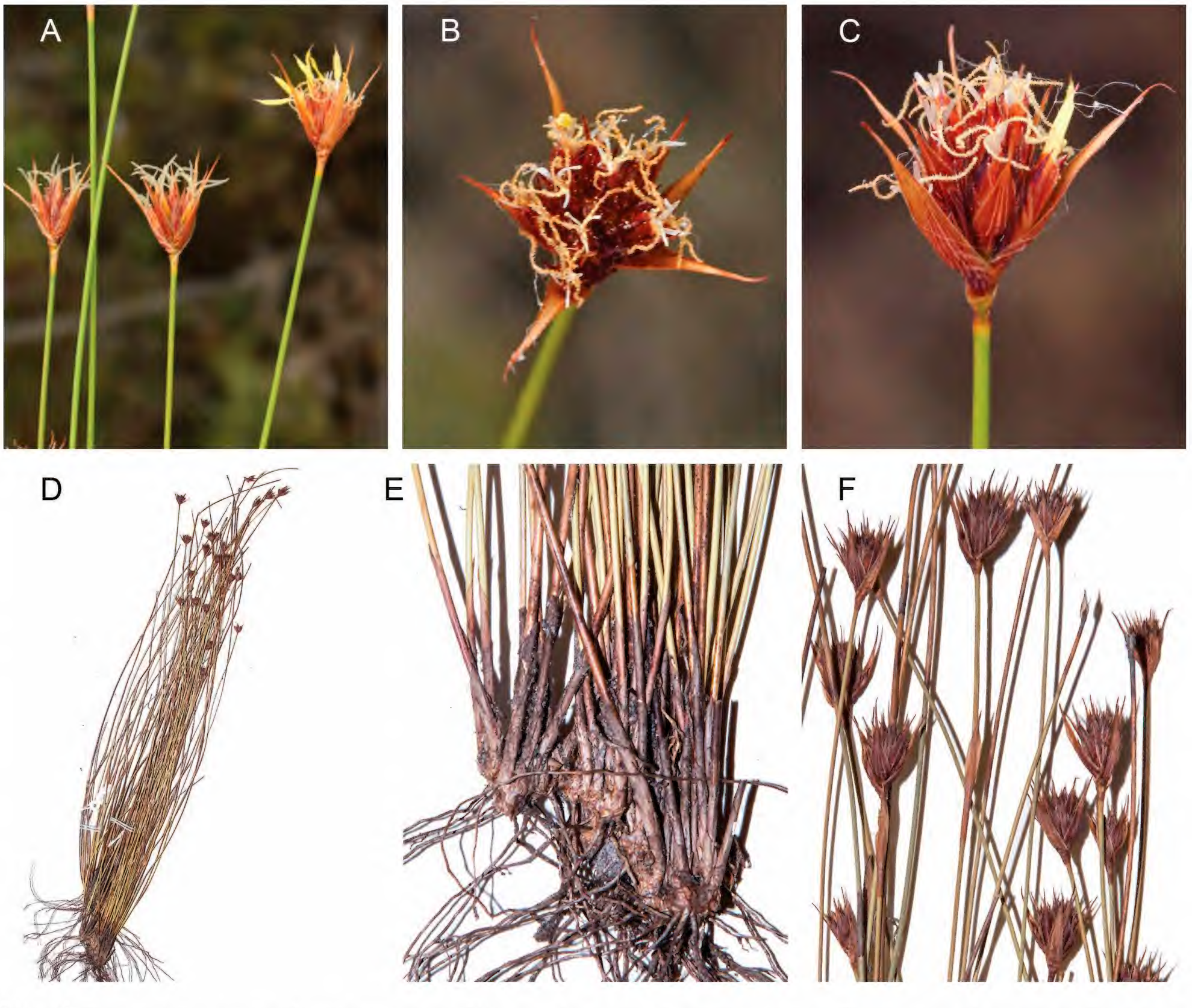

Fig. 19. *Tricostularia davisii*. Near Cape Riche, Western Australia. A–C: Flowering inflorescence. D. Habit. E. Plant base. F. Inflorescence. Vouchers: A–C: *G. Byrne 4937* (PERTH); D, E: *K. Newbey 4616*; F: *K.L. Wilson 2937* (NSW). Photos A–C by G. Byrne; D–F by R.L. Barrett.

Conservation status: Known from just eleven populations, two of which are roadsides, but conserved in Stirling Range National Park, Mount Manypeaks Nature Reserve, and two additional gazetted Nature Reserves. Further targeted surveys are warranted, but the species is probably not currently threatened. IUCN: Data Deficient.

Specimens examined: WESTERN AUSTRALIA: 4.3 km from the Cape Riche Camping Ground on Sandalwood Road, 27 Oct. 2013, *G. Byrne 4937* (PERTH); *c.* 22 km NE of Manypeaks, on Drawbin Road, *c.* 6 km from Pfeiffer Road, 4 Oct. 1976, *B.G. Briggs 6596* (NSW, PERTH); 90 km NE of Albany, 8 Nov. 1978, *R.J. Cranfield 1118* (MEL, NSW, PERTH); Seed orchard in gravel pit, 10 km from Hassell Highway, on Cheyne Beach Road, E of Albany, 8 Oct. 1997, *E.J. Croxford* 7962 (PERTH); Intersection McGregor Road and Governor Broome Road, Scott River Sandplain, 25 Nov. 1976, *G.J. Keighery 960* (PERTH); Forest Grove Road, 8 km SW [of] Witchcliffe, 18 Nov. 1980, *G.J. Keighery 3599* (PERTH); Western slopes Mount Manypeaks, 27 Nov. 1986, *G.J. Keighery 8829* (NSW, PERTH); Gazetted Reserve 13240, Cheyne Bay, N of Cape Riche, 24 Oct. 1996, *J.W. Mercer 87* (PERTH); 22 km NW of Cape Riche, 27 Nov. 1974, *K.R. Newbey 4616* (NSW, PERTH); Roadside along Toolbrunup Road, *c.* 1.3 km W from the intersection with Chester Pass Road, Stirling Range National Park, 15 Oct. 2007, *A.J. Perkins s.n.* (NSW 872772, PERTH, SYD); Gazetted Reserve 26688 on South Stirling Road, 3.3 km N of junction with Pfeiffer Road, 20 Oct. 1999, *E.M. Sandiford EMS 460* (PERTH); *c.* 5 km NW of Cape Riche on Wellstead road, 16 Oct. 1979, *K.L. Wilson 2937* (NSW, PERTH).

Etymology: In recognition of the work of Robert (Rob) W. Davis (1959–), botanist at the Western Australian Herbarium, in documenting the flora of Western Australia, especially the genus *Ptilotus* (Amaranthaceae; e.g. Hammer *et al.* 2019).

Common name: Davis' Tricostularia.

Notes: A very distinctive species with superficial resemblance to *Chaetospora* R.Br. due to the subcapitate heads and floral bracts that exceed the spikelets. Previously confused with *T. compressa* as it was often assumed

these were immature plants of that species. Two disjunct collections, from near Beenup and Witchcliffe, are immature and are only tentatively included in this taxon.

Tricostularia drummondii (Steud.) R.L.Barrett & K.L.Wilson, *comb. nov*.

Basionym: *Discopodium drummondii* Steud., *Syn. Pl. Glum*. 2(8–9): 150 (1855).

Type citation: "Hrbr. Drummond coll. III. 328 et 329. N. Holl."

Type: Western Australia: [Swan River Colony, 1845], *J. Drummond* (3rd collection) *329* (lectotype (here designated): P 00603255; isolecto: G 00195298, G 00195299, G 00195300 (2 sheets), K 000960118, P, PERTH 2334488).

Excluded syntype (= *T. newbeyi*): Western Australia: [Swan River Colony, between Albany, Stirling Range, and Cape Riche, *c*. Aug. 1844], *J. Drummond 328* (3rd collection) (syn: BM, G 00195294 (2 sheets), G 00195295, G 00195296 (2 sheets), K 000960119, K 000960120, MEL 2204195, P 00603254, P 01926655, PERTH 2334828, TCD, *n.v.*).

Illustration: Wheeler and Graham (2002; fig. p. 298, right-hand inflorescence only, as *T. neesii*).

Insufficient material was available at NSW to complete a description.

Diagnostic characters: Related to *T. exsul*, differing in the shorter inflorescence (3–4 cm long) with fewer, finer spikelets. (Figure 20).

Fig. 20. *Tricostularia drummondii*. Near Beverley, Western Australia. A. Habit. B. Plant base. C. Inflorescence. Voucher: *N. Gibson 4035* (NSW). Photos by R.L. Barrett.

Distribution: Endemic to the south-west of Western Australia, between Perth and Arthur River.

Habitat: Grows in low woodland or mallee over sand or laterite, on flats, rises or sometimes in swampy areas. Recorded in association with *Banksia attenuata*, *B. menziesii*, *Conostylis serrulata*, *Cyathochaeta stipoides*, *Eremaea pauciflora*, *Eucalyptus marginata*, *E. wandoo*, *Evandra aristata*, *Ficinia nodosa*, *Gymnoschoenus anceps*, *Hibbertia subvaginata*, *Jacksonia hakeoides*, *Lambertia inermis*, *Phlebocarya ciliata*, Restionaceae, *Schoenus asperocarpus*, *S.* aff. *pedicellatus* and *S. sublateralis*.

Phenology: Flowers probably in spring.

Conservation status: Poorly known and further assessments are required. IUCN: Data Deficient.

Specimens examined: WESTERN AUSTRALIA: 2 miles NNE of Yeal Swamp in Wanneroo Forestry Reserve, 24 Feb. 1965, *Y. Chadwick 2565* (PERTH); on the western boundary of the reserve, 1.4 km N of Kempton Road, Wandoo Conservation Park, *c*. 27 km WSW of Beverley [Plot - YO14], 11 Sept. 1997, *N. Gibson 4035* (NSW, PERTH); Gazetted Reserve 9098; *c*. 16–19 km W of Wagin towards Arthur River, 26 Nov. 1984, *G.J. Keighery 7418* (PERTH); Talbot Road Reserve, Middle Swan, Midland, 6 Nov. 1990, *G.J. Keighery 11836* (PERTH); N of Matthew Road, *c*. 1.4 km W of Cunderdin-Wyalkatchem Road, *c*. 25 km N of Cunderdin, 20 Oct. 1997, *B.J. Lepschi, T.R. Lally & W.H. Treasure BJL 3577* (PERTH); Dryandra State Forest, 30 Dec. 1987, *D.M. Rose 602* (PERTH).

Etymology: Named for botanist James Drummond (1786–1863), a prolific collector of plants from the fledgling Swan River Colony from 1836 to 1852 (Erickson 1969; Barker 2005).

Common name: Drummond's Tricostularia.

Notes: While the generic name *Discopodium* Steud. is illegitimate, being a later homonym, the species name is validly published (Art. 55.1; Turland *et al.* 2018). The two cited specimens are here considered to belong to two distinct species. A lectotype is designated to fix the application of the name. P 00603255 is chosen as it is from Steudel's herbarium. Bentham (1878) considered the two syntypes to be referrable to *T. compressa* and *T. neesii*, but both specimens are here considered distinct from each of these species, and a new combination is made for *Discopodium drummondii* with one syntype as the lectotype, while the residual syntype is here assigned to a new species, *T. newbeyi*.

Tricostularia exsul (C.B.Clarke) K.L.Wilson & R.L.Barrett, *Austral. Syst. Bot.* 25: 286 (2012).

Lepidosperma exsul C.B.Clarke, *Kew Bull. Misc. Inf. Add. Ser.* 8: 47 (1908).

Type citation: 'AUSTRALIA. Swan River, Drummond, n. 330 (hb. DC.).'

Type: WESTERN AUSTRALIA. Swan River [colony], 1845, *J. Drummond 330* (lectotype (here designated): G-DC 00195302; isolecto: B 10 0277894 (fragment), G-DC 00195301, G-DC 00195303, K 000960117, K (ex TCD); P; TCD, *n.v.*).

Tricostularia neesii var. *elatior* Benth., *Fl. Austral.* 7: 384 (1878).

Type citation: 'Drummond, n. 322.'

Type: Western Australia: Swan River [colony], 1845, *J. Drummond 322* (holo: K 000960116!).

Perennial tufted herb, 0.4–1(–1.3) m high; plants clonal, forming dense tussocks 0.2–1.2 m across; rhizome thin, woody, short, branched, 1.6–2.3 mm diam., non- or slightly pseudobulbous; old leaf sheaths covering the rhizome, breaking apart into fine fibres with age, pale brown; roots sand-binding. *Culms* slender, rigid, erect, with 2 nodes, terete, finely striate, 35–90(–120) cm tall, 1.1–2.0 mm diam., smooth, glabrous, dull to bright medium green to yellow-green, base not enlarged, but noticeably thicker than apex. *Leaves* mostly basal, numerous, and 2 cauline; phyllotaxy loosely spirotristichous; sheath 33–80 mm long, 1.5–2.3 mm wide, broader than the leaf lamina, margins finely scabrid, otherwise glabrous, straw-coloured to reddish brown, dull, upper margin membranous, oblique, finely scabrid, ligule absent; cauline sheath tight around culm; *pseudopetiole* obscure or absent; basal leaves with a much reduced lamina, not exceeding the culms, lamina dorsiventral, 0.1–0.2 cm long, 0.4–0.6 mm wide; bases brown-membranous, not dividing; lamina ± linear or narrowly triangular, ± flat, ± flexuous, old leaf tips not curling, finely multi-striate, margins very finely scabrid (only visible at (40×), otherwise glabrous, brown, concolorous, weakly keeled along mid-nerve, margins not recurved, apex acute; lowest leaves reduced to a sheath, lacking a lamina, pale to reddish brown. *Inflorescence* elongate, panicle-like, narrow, somewhat flexuous, with 5–9 nodes, 8–12 cm long, 4–9 mm wide, sometimes interrupted at the base, axis green or yellow-green, not glaucous; bracts reduced leaf-like, ± equal the spikelet clusters, sheaths open, partly enveloping the higher bracts, gradually reducing along the inflorescence, basal bract much shorter than inflorescence, 20–30 mm long; branches erect, with usually 3 but up to 7 spikelets, spikelet(s) on short, compressed, scabrous peduncles 1–3 mm long, arising in each bract axil; basal branchlet 20–29 mm long; spikelet prophyll present, sheath 6.2–8.4 mm long, brown, with 3 distinct veins and many fine striations, partially enclosing the spikelet, with a slender lamina 3.3–4.6 mm long, brown. *Spikelets* brown, lanceolate, 8.5–11 mm long, 2.1–3.3 mm wide, subterete, with 5 or 6 glumes, only topmost 3 fertile, the lower flower male, sterile, the second flower male, fertile, the upper flower bisexual, fertile, sometimes with a highly reduced glume above the florets; glumes distichous, basal glume 3.6–4.2 mm long, fertile glumes 7.0–8.8 mm long, 1.3–2.2 mm wide, membranous, pale reddish brown, sometimes translucent, sparsely scabrous on the keel and margins, lamina glabrous, lanceolate, acuminate, with a mucro 0.3–1.0 mm long, keel distinct; rachilla compact and not sinuous in fruiting spikelets. *Perianth segments* 6, whitish, minute, 0.7–2.0 mm long, ± filiform, expanded below, tapering to a fine point, sparsely scabrous. *Stamens* 3; anther connective 5.9–7.8 mm long, subulate; anthers yellow, 3.6–4.1 mm long, with a glabrous apical appendage 0.8–1.2 mm long. *Style* trifid, base 3.6–4.1 mm long, glabrous, slender above and below (dilated on nutlet apex), branches 2.8–3.2 mm long, hispidulous. *Nutlet* shortly stipitate, stipe 0.5–0.6 mm long, somewhat constricted, broad ellipsoid, obscurely trigonous, dull, mid-brown to dark brown, 2.5–2.8 mm long including the stipe and style base, 1.3–1.5 mm diam., faces smooth, puberulous, densely so near apex, epidermal cells square–hexagonal, inconspicuous, with three fine white ribs, style base distinctly enlarged, thick, persistent, shortly conical; embryo not examined. Photosynthetic pathway not examined. (Figure 21).

Fig. 21. *Tricostularia exsul*. Albany, Western Australia. A. Habit. B. Plant base. C. Inflorescence. Voucher: *C.R.P. Andrews s.n*. (NSW 687651). Photos by R.L. Barrett.

Diagnostic characters: Similar to *T. drummondii*, *T.* sp. Albany and *T.* sp. Two Peoples Bay, differing in the more robust rhizomes (1.6–2.3 mm diam.) and culms (1.1–2.0 mm diam.), and the larger inflorescences (8–12 cm long).

Distribution: Endemic to the south-west of Western Australia, between Albany and Manypeaks.

Habitat: Grows in swampy areas in heath on deep white or grey sands or clay loams. Recorded in association with *Acacia robiniae*, *Actinodium cunninghamii*, *Anarthria scabra*, *Aotus intermedia*, *Boronia crenulata*, *Callistemon glaucus*, *Cyathochaeta avenacea*, *Darwinia vestita*, *Daviesia incrassata*, *Eucalyptus marginata*, *E. staeri*, *Evandra pauciflora*, *Gompholobium scabrum*, *G. venustum*, *Hibbertia pulchra*, *Homalosermum firmum*, *Hovea chorizemifolia*, *Isopogon formosus*, *Latrobea diosmifolia*, *L. genistioides*, *L.* sp. South Coast (A.M.Ashby 1949), *Lepidosperma drummondii*, *L.* cf. *pubisquameum*, *L. striatum*, *L. ustulatum*, *L.* sp. Dunns Swamp (R.Davis 724), *Leucopogon glabellus*, *Lomandra nigricans*, *Melaleuca thymoides*, *Mesomelaena stygia*, *M. tetragona*, *Microtis atrata*, *Morelotia octandra*, *Pultenaea reticulata*, *Quinetia urvillei*, Restionaceae, *Schoenus armeria*, *S. globifer, S. obtusifolius*, *S. racemosus*, *Sphaerolobium hygrophyllum*, *S. pubescens*, *Stylidium assimile*, *S. luteum*, *Synaphea polymorpha* and *Tetratheca setigera*.

Phenology: Flowers recorded for November–December.

Conservation status: Poorly known and further surveys are recommended. Known to occur in Bakers Junction Nature Reserve where it is locally common. IUCN: Data Deficient.

Selected specimens examined: WESTERN AUSTRALIA: Albany, Dec. 1902, *C.R.P. Andrews s.n.* (NSW 687651); Bakers Junction Nature Reserve, N of Albany, 20 May 2008, *R.L. Barrett, E.M. Sandiford & D. Rathbone RLB 5020* (PERTH); South Coast Highway, 0.9 km SW of Homestead Road turn-off, 3 km SW of Manypeaks village, 22 Nov. 1994, *K.L. Wilson 9095 & K. Frank* (NSW).

Etymology: From the Latin *exsul* (exile), in reference to the fact that George Bentham had inadvertently sent the specimen originally at K to G (according to Clarke's annotation on the sheet in K) apparently thinking it represented a common species, leaving no material of the species at K, thus it was exiled to Geneva (Clarke 1908).

Common name: Robust Tricostularia.

Notes: A lectotype is selected for *Lepidosperma exsul* C.B.Clarke as, while Clarke (1908) specified material at G-DC, there are three sheets held at G-DC, and additional material at K (one sheet ex G-DC, ironically originally ex K), P and TCD. There may well be additional sheets that we are yet to trace as Drummond commonly collected many duplicates (see Barrett and Wilson 2012). We choose G-DC 00195302 as the lectotype as this sheet has the amplest material and an annotation by Clarke.

Wilson (1980) recognised that *Tricostularia neesii* var. *elatior* Benth. was the same as *T. exsul*, but species limits within *Tricostularia* were too poorly understood at that time to reinstate *T. exsul* (at that time known as *Lepidosperma exsul*).

Tricostularia lepschii R.L.Barrett & K.L.Wilson, *sp. nov.*

Type: Western Australia: *c.* 17.5 km W of Lake King township on road to Newdegate, 19 Oct. 1995, *B.J. Lepschi 2199* (holo: PERTH 4121643; iso: CANB 540114, NSW 687398).

Tricostularia sp. Lake King (A.M. Coates 2298), *FloraBase* (2008–), accessed 4 June 2020.

Perennial tufted herb, 0.15–0.4 m high; plants clonal, forming spreading tussocks *c.* 0.1–0.2 m across, culms in tight clumps, distinctly spaced at *c.* 1 cm intervals; rhizome thin, woody, short, branched, 1–2.6 mm diam., non-pseudobulbous; old leaf sheaths covering the rhizome, sometimes breaking apart into fine fibres with age, pale brown; roots sand-binding. *Culms* slender, rigid, erect, not noded, terete, very finely striate, 0.6–0.8 mm diam., smooth, glabrous, bright light green to yellow-green, base not enlarged. *Leaves* all basal, few; phyllotaxy loosely spirotristichous; sheath 14–59 mm long, 0.8–1.0 mm wide, slightly broader than the leaf lamina, margins glabrous, straw-coloured to pale brown, dull, upper margin membranous, oblique, glabrous or very finely ciliate, ligule absent; cauline sheath tight around culm; *pseudopetiole* obscure to distinct, semi-terete, up to 2.5 mm long; basal leaves with a much reduced lamina, not exceeding the culms, lamina dorsiventral, 0.25–0.35 cm long, 0.25–0.35 mm wide; bases white-membranous below pseudopetiole, not dividing; lamina ± linear, ± flat to slightly channelled, ± flexuous, old leaf tips not curling, finely multi-striate, margins finely scabrid, otherwise glabrous when young, green, concolorous, not keeled along mid-nerve, nerves obscure, margins not ribbed, finely scabrous, not recurved, apex long-attenuate, ± acute; lowest leaves reduced to a sheath, lacking a lamina, pale brown. *Inflorescence* very contracted panicle-like, subcapitate, with 1 or 2(?3) nodes, but very compact so nodes obscured by spikelets, 0.7–1.1 cm long, 4–8 mm wide, not interrupted, axis green or yellow-green, not glaucous; bracts reduced leaf-like, shorter than or equal to the spikelet clusters, sheaths open, not or somewhat enveloping the higher bracts, gradually reducing along the inflorescence, basal bract ± equal to inflorescence, 6–8 mm long; branches erect, with 2–4 spikelets in a terminal cluster, spikelets sub-fasciculate, on short, terete, glabrous peduncles 0.5–1 mm long, arising in each bract axil; cladoprophyll subtending each spikelet bract-like, sheath 3.1–3.6 mm long, brown, with a distinct midrib, partially enclosing the spikelet, with a slender lamina 0.9–1.2 mm long, brown. *Spikelets* brown, lanceolate, 4–6 mm long, compressed, with 6 glumes, only topmost 2 fertile, both bisexual, fertile, or the lower flower male, fertile, no reduced glume above the florets; glumes ± distichous, basal glume 1.5–3.0 mm long, fertile glumes 4.0–4.5 mm long, 1.0–1.1 mm wide, membranous, red-brown to dark red-brown, sparsely and finely scabrous on the keel, lamina glabrous, ovate-lanceolate, acute to acuminate, with a mucro to 0.6 mm long, keel distinct; rachilla compact and not or scarcely sinuous in fruiting spikelets, but the two fertile flowers presented beside each-other, so rachilla appearing flared at the apex. *Perianth segments* 6, whitish, minute, 0.4–1.1 mm long, compressed to ± filiform, expanded below, tapering to a fine point with a few apical hairs. *Stamens* 3; anther connective [not seen mature]; anthers 1.5–2.2 mm long, with a glabrous apical appendage up to 0.3 mm long. *Style* [not seen]. *Nutlet* shortly stipitate, stipe *c.* 0.3 mm long, scarcely constricted, broad ellipsoid, obscurely trigonous, dull, mid-brown, *c.* 2.0 mm long including the stipe and style base, *c.* 1.3 mm diam., faces smooth, finely puberulous, epidermal cells square–hexagonal, inconspicuous, with three fine white ribs, style base not enlarged; embryo not examined. Photosynthetic pathway not examined. *2n* = unknown. (Figure 22).

Diagnostic characters: Related to *T. neesii*, differing in the elongate rhizomes with tight clusters of culms at *c.* 1 cm intervals, thin culms without nodes, sub-capitate inflorescences and short inflorescence bracts. The two fertile flowers presented beside each other, so the rachilla appears flared at the apex, is unusual in the genus.

Distribution: Endemic to the south-west of Western Australia, between Kulin, Lake King and south towards Ravensthorpe.

Habitat: Grows in well-drained, deep, white, grey, or brown sands on flats or consolidated dunes, sometimes with laterite gravel or over clay in mixed open low scrub. Recorded in association with *Banksia* spp., *Callistemon phoeniceus*, *Conostylis* sp., *Eremaea* sp., *Eucalyptus tetragona*, *Grevillea* sp., *Hakea* spp., *Lepidosperma carphoides*, *L.* sp. Clathrate (R.L.Barrett & G.F.Craig RLB 3570), *L.* sp. Jerdacuttup (R.L.Barrett RLB 2770), *L.* sp. P2 Capitate (K.L.Wilson 2798), *Leptospermum spinescens*, *Melaleuca* spp., *Mesomelaena stygia*, *Schoenus caespititius*, *S. cygneus*, *S.* sp., *Tricostularia bennettiana* and *Verticordia* sp.

Phenology: Flowers probably August–October.

Conservation status: Recorded as locally common, particularly in disturbed areas, but only known from about six populations in the vicinity of Lake King (between Kulin and Ravensthorpe). Conservation Codes for Western Australian Flora: Priority 2 (as *Tricostularia* sp. Lake King (A.M. Coates 2298)). IUCN: Data Deficient.

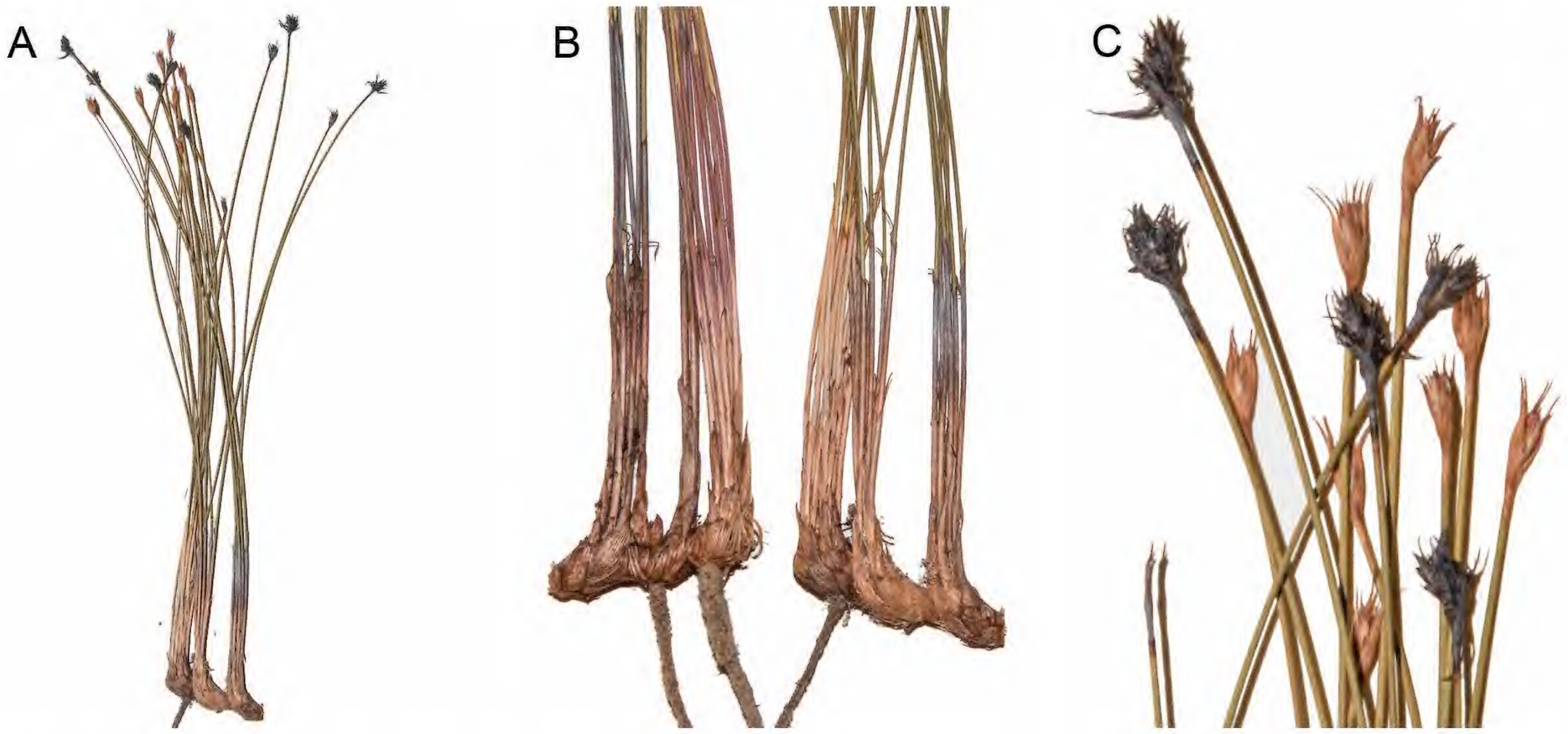

Fig. 22. *Tricostularia lepschii*. Near Lake King, Western Australia. A. Habit. B. Plant base. C. Inflorescence. Voucher: *B.J. Lepschi 2199* (NSW). Photos by R.L. Barrett.

Specimens examined: WESTERN AUSTRALIA: [precise localities withheld for conservation reasons]: near Kulin, Aug. 1998, *E. Bennett & K. Del Fante DS 19.15* (PERTH); near Lake Grace, June 1991, *A.M. Coates 2298* (PERTH); near Ravensthorpe, Nov. 2016, *D. Coultas DC-01* (PERTH); near Ravensthorpe, Sept. 2014, *D. Coultas SC-05-02* (PERTH); near Kulin, Aug. 2000, *G.J. Keighery & N. Gibson 5280* (PERTH); near Lake Grace, Sept. 1997, *G.J. Keighery & N. Gibson 5283* (PERTH); NE of Lake King, 16 Nov. 1980, *K.R. Newbey 8030* (NSW, PERTH); SSE of Lake King, 28 Aug. 1973, *M.D. Tindale 3788* (CANB, K, NSW, P, PERTH); S of Lake King, 6 Nov. 1994, *K.L. Wilson 8779 & K. Frank* (NSW, PERTH).

Etymology: Named for Brendan J. Lepschi (1969–), for his enthusiastic support and efforts to tackle curly nomenclatural issues in the Australian flora, and his wide collecting, including this obscure species. He is the author of a number of classic botanical publications including *The taller tree of liff* (Lepschi 2012).

Common name: Lepschi's Tricostularia.

Notes: Occasionally confused with *Schoenus globifer* Nees due to superficial similarities in the plant habit. Only immature and old spikelets have been observed, so several floral and fruiting characters remain poorly known. A few spikelets on *M.D.Tindale 3788* (NSW) are infected by a smut fungus, *Moreaua tricostulariae* (Websdane & Vánky) Vánky (see Vánky and Shivas 2008).

Tricostularia neesii Lehm., *Nov. Stirp. Pug.* 8: 52 (1844).

Chaetospora neesii (Lehm.) Boeckeler, *Linnaea* 38(3): 297 (1874). *Schoenus neesii* (Lehm.) F.Muell., *Syst. Census Austral. Pl.* 1: 128 (1882).

Type citation: "Habitat in Australia occidentali. (Herb. Preiss no. 1728.) Colitur in hort. bot. Hamburg."

Type: Western Australia: Swan River, 1843, [*J.A.*]*L. Preiss* [*Pl. Preissianae No. 1728*] (lectotype (here designated): LD 1730387; isolecto: G-DC 00195297, MEL 2297589, MEL 2297590).

Possible syntype: Cultivated at Hamburg Botanic Garden (?syn: ?HBG, *n.v.*).

Illustration: Wheeler and Graham (2002; fig. p. 298, excluding the two inflorescence figures); Barrett and Pin Tay (2016; pl. 4–6, p. 203).

Perennial tufted herb, 0.5–0.8 m high; plants clonal, forming dense tussocks 0.3–0.8 m across; rhizome thin, woody, short, branched, 0.9–1.6 mm diam., non-pseudobulbous; old leaf sheaths covering the rhizome, not breaking apart into fine fibres with age, pale to reddish brown; roots sand-binding. *Culms* slender, rigid, erect to spreading, usually not noded, but sometimes with 1 or 2 nodes terete, very finely striate, 0.5–1.5 mm diam., smooth, glabrous, bright green to yellow-green, base not enlarged. *Leaves* mostly basal, numerous, and 1 or 2 cauline; phyllotaxy loosely spirotristichous; sheath 12–100 mm long, 0.7–1.5 mm wide, slightly broader than the leaf lamina, margins with just a few very fine scabrid hairs, otherwise glabrous, straw-coloured to reddish brown, dull, upper margin membranous, oblique, ligule absent; cauline sheath tight around culm; *pseudopetiole* obscure or absent; basal leaves with a much reduced lamina, much shorter than the culms, lamina dorsiventral, 3–5 mm long, 0.2–0.4 mm wide; bases pale brown-membranous, not dividing; lamina

± linear, not channelled, ± flexuous, old leaf tips not curling, finely multi-striate, margins sometimes very finely scabrid, otherwise glabrous, green, concolorous, weakly keeled along mid-nerve, margins not recurved, apex attenuate; lowest leaves reduced to a sheath, lacking a lamina, pale to reddish brown. *Inflorescence* much-contracted, panicle-like, narrow-oblate to lanceolate, not flexuous, with 2–4-nodes, 1.5–2.2 cm long, 4–6 mm wide, not interrupted, axis ± fully concealed, green or yellow-green, not glaucous; bracts bract-like, usually shortly exceeding the spikelet clusters, sheaths open, partially enveloping the higher bracts, gradually reducing along the inflorescence, basal bract much shorter than inflorescence, 8–12 mm long; basal branchlet 10–15 mm long, branches erect, with solitary or 2 spikelets per branchlet, spikelet(s) ± sessile or on short, compressed, glabrous peduncles to 0.5 mm long, arising in each bract axil; spikelet prophyll present, sheath 3.1–4.6 mm long, translucent to pale brown or with dark reddish flecks, with distinct mid-vein, partially enclosing the spikelet, with a slender lamina 0.9–1.5 mm long, translucent to pale brown. *Spikelets* translucent to pale brown or with dark reddish flecks, lanceolate, 5.5–6.8 mm long, 1.1–1.7 mm wide, somewhat compressed, with 5 or 6 persistent glumes, only topmost 2 fertile, the lower flower male fertile, the upper flower bisexual, fertile, no reduced glume above the florets; glumes distichous, basal glume 3.6–4.5 mm long, fertile glumes 4.7–5.8 mm long, 0.9–1.3 mm wide, membranous, translucent to pale brown or with dark reddish flecks, very finely ciliate on the keel and margins, the hairs short and spreading, face glabrous, ovate-lanceolate, acuminate, with a mucro 0.6–1.2 mm long, keel distinct; rachilla compact and not sinuous in fruiting spikelets. *Perianth segments* 6, whitish, 0.5–1.2 mm long, ± filiform but dilated at the very base, tapering to a fine point with a few minute hairs at the apex. *Stamens* 3, anther connective 3.1–4.6 mm long, subulate; anthers yellow, 2.7–3.4 mm long, with a glabrous apical appendage 0.4–0.5 mm long. *Style* trifid, base 3.0–3.5 mm long, glabrous, slender above, not or scarcely dilated below, branches 2.4–2.8 mm long, hispidulous. *Nutlet* shortly stipitate, stipe *c.* 0.4 mm long, somewhat constricted, obovoid to obpyriform, obscurely trigonous, dull, mid-brown, 1.9–2.2 mm long including the stipe and style base, 0.8–1.0 mm diam., faces smooth, very minutely puberulous especially near apex, epidermal cells square–hexagonal, inconspicuous, with three fine white ribs, style base not enlarged, cap-like; embryo not examined. Photosynthetic pathway not examined. (Figure 23).

Fig. 23. *Tricostularia neesii*. A. Habit, Armadale, Western Australia. B. Plant base. C. Inflorescences. D. Inflorescence. Vouchers: A, B: *F. Hort & J. Hort 2452* (NSW); C: *J. Pryde & M. Morley MM 12* (NSW). D. Darling Range (not vouchered). Photos by R.L. Barrett.

Diagnostic characters: Distinguished by the relatively short, compact inflorescence and culms with 0, 1 or 2 nodes.

Distribution: Endemic to the south-west of Western Australia where it is widespread, from Eneabba south to Bunbury and east to Ravensthorpe, extending inland along the Avon River and to the Stirling Range.

Habitat: Grows in open shrubland and heath in seasonal wetlands and damplands, usually on sandy loam, sometimes in white or grey sand over laterite. Recorded in association with *Allocasuarina humilis*, *Anarthria laevis*, *A. gracilis*, *Banksia attenuata*, *Byblis gigantea*, *Caustis dioica*, *C. gigas*, *Chordifex microcodon*, *Conostylis* sp., *Corymbia calophylla*, *Eucalyptus accedens*, *E. marginata*, *E. wandoo*, *Hakea ceratophylla*, *H. gilbertii*, *H. prostrata*, *Kingia australis*, *Lepidosperma* aff. *scabrum*, *L.* aff. *squamatum*, *Melaleuca* sp., *Mesomelaena pseudostygia*, *M. tetragona*, *Morelotia australiensis*, *Pericalymma ellipticum*, *Petrophile filifolia*, *Schoenus insolitus*, *S.* sp. Ciliate Sheaths (K Newbey 9402) and *Xanthorrhoea preissii*.

Phenology: Flowers October–December.

Conservation status: Widespread and not considered threatened. Protected in numerous conservation areas including Alexander Morrison National Park and Badgingarra National Park. IUCN: Least Concern.

Selected specimens examined: WESTERN AUSTRALIA: 3.2 km W of Brand Highway on Bibby Road (N side), Badgingarra National Park, 21 Oct. 2008, *R.L. Barrett & B.G. Briggs RLB 5302* (PERTH); Alexander Morrison National Park, 200 m along firebreak which intersects with Coorow–Greenhead Road, 3.4 km E of junction with Tootbardi Road, 17 Nov. 2008, *M. Hislop 3865* (PERTH); Brookton Highway, Armidale, S side of highway, 1.5 km E of Omeo Road, 7 Dec. 2004, *F. Hort & J. Hort 2452* (NSW, PERTH); On W side of Tribune Road, 1 km S of private property boundary. State Forest, *c.* 33 km W of Beverley [Plot YO27], 26 Oct. 2000, *G.J. Keighery & N Gibson 5281* (PERTH); Korijekup Nature Reserve; SE of Harvey, 13 May 2007, *G.J. Keighery & B.J. Keighery 1028* (PERTH); Kelmscott, 20 Nov. 1899, *A. Morrison s.n.* (E 00688606*); Cannington, 21 Nov. 1910, *A. Morrison s.n.* (E 00688607*, NSW 687623); Watkins Plot 3, Watkins Road Bush Forever site, 6 Nov. 2006, *J. Pryde & M. Morley MM 12* (NSW, PERTH); NE corner of Wandoo National Park, N of Dobaderry Road and S of Kokendin Road, 7 Jan. 2008, *M. Wheeler 57* (MEL, PERTH); Alexander Morrison National Park, 30 km E of Brand Highway on the Greenhead to Coorow road, 8 Nov. 1994, *K.L. Wilson 8819 & K. Frank* (NE, NSW, PERTH); Doyle Road, 5.8 km E of junction with Bokal Road South, SW of Arthur River, 6 Oct. 2014, *K.L. Wilson 11267 & A. Wilson* (CANB, K, NE, NSW, PERTH, PRE).

Etymology: Named for Christian Gottfried Daniel Nees von Esenbeck (1776–1858), a German botanist who contributed greatly to the systematics of Cyperaceae (e.g. Nees 1832, 1834, 1835, 1841, 1846).

Common name: Nees' Tricostularia.

Notes: This name has been broadly applied to many of the Western Australian taxa recognised in the genus, particularly any taxa with a slender inflorescence, but the type specimen actually has quite short, compact inflorescences.

A lectotype is selected as the protologue states that material cultivated ('colitur') at Hamburg Botanic Garden was also examined, though no voucher specimen has been traced and it is possible that no voucher was made from the cultivated material. Lehmann probably saw a specimen at either B or S, but we have not located material at either herbarium, so we designate a specimen at LD (LD 1730387) as the lectotype as it is a good specimen in the primary *Plantae Preissianae* set of collections.

Most collections have no nodes on the culms. A few collections have one or rarely two nodes on the culms, and most of these are from the vicinity of the Stirling Range, but a few are from near Perth and the northern Sandplain. Further fieldwork is required to determine whether there is any taxonomic significance to this variation.

Tricostularia newbeyi R.L.Barrett & K.L.Wilson, *sp. nov*.

Type: Western Australia: Dola Reserve, Honey Drive, 2.13 km N of Rabbit Proof Fence road, near North Ongerup telephone exchange, 8 Jan. 2006, *L. Strahan 409* (holo: PERTH 7456336).

Tricostularia sp. Ongerup (L. Strahan 409), *FloraBase* (2008–), accessed 4 June 2020.

Perennial tufted herb, 0.2–0.9 m high; plants clonal, forming dense tussocks 0.2–1 m across; rhizome thin, woody, short, branched, 1.5–2.5 mm diam., non- or slightly pseudobulbous; old leaf sheaths covering the rhizome, not breaking apart into fine fibres with age, pale brown; roots sand-binding. *Stems* slender, rigid, erect to spreading, often arcuate, with 1 (or 2) nodes, terete, very finely striate, 0.5–1.2 mm diam., smooth, glabrous, green to yellow-green, base not enlarged. *Leaves* mostly basal, numerous, and 1 (or 2) cauline; phyllotaxy loosely spirotristichous; sheath 15–25 mm long, 1.2–1.8 mm wide, slightly broader than the leaf lamina, margins with a few minute scabrid hairs, otherwise glabrous, straw-coloured to reddish brown, dull, upper margin membranous, oblique, finely scaberulous, ligule absent; cauline sheath tight around culm; *pseudopetiole* obscure or absent; basal leaves with a much reduced lamina, not exceeding the culms, lamina dorsiventral, 0.1–0.2 cm long, c. 0.05 mm wide; bases white-membranous, not dividing; lamina ± triangular, ± flat, not flexuous, old leaf tips not curling, finely multi-striate, margins finely scaberulous, otherwise glabrous when young, green, concolorous, weakly keeled along mid-nerve, margins ribbed and finely scaberulous, not recurved, apex acute; lowest leaves reduced to a sheath, lacking a lamina, pale brown. *Inflorescence* panicle-like, narrow, somewhat flexuous, with 6–9 nodes, 1.5–6 cm long, 5–8 mm wide, sometimes interrupted, axis green or yellow-green, not glaucous; bracts reduced leaf-like, not exceeding the spikelet clusters, sheaths open, not enveloping the higher bracts, gradually reducing along the inflorescence, basal bract much shorter than inflorescence, 7–13 mm long; branches erect, with (1–)2–4 fasciculate spikelets in 6–9 clusters, spikelets on short, compressed, glabrous peduncles 0.5–1.5 mm long, arising in each bract axil; cladoprophyll subtending each spikelet bract-like, sheath 3.0–4.0 mm long, pale brown to brown, with 3 distinct veins, partially enclosing

the spikelet, with a slender lamina 0.7–1.0 mm long, brown. *Spikelets* pale brown to mid-brown, lanceolate, 4.4–5.6 mm long, terete, with 6 or 7 glumes, only topmost 2 fertile, the lower flower bisexual, female sterile, the upper flower bisexual, fertile, with a reduced glume above the florets to 2.3 mm long; glumes distichous, basal glume 2.9–3.4 mm long, fertile glumes 3.5–5.0 mm long, 1.1–1.6 mm wide, membranous, pale brown to mid-brown (apex often darker than body and keel paler yellow-brown), glabrous or finely ciliate on the keel and margins, lamina glabrous, ovate-lanceolate, acuminate, with a mucro to 0.8 mm long, keel distinct; rachilla compact and not or scarcely sinuous in fruiting spikelets. *Perianth segments* 6, whitish, minute, 0.5–1.1 mm long, expanded below, tapering to a fine point with a few stiff apical hairs. *Stamens* 3; anther connective 4.1–5.5 mm long, subulate; anthers yellow, *c*. 2.0 mm long, with a glabrous apical appendage up to 0.3 mm long. *Style* trifid, base 1.5–2.4 mm long, hispidulous and slightly flared in apical third, glabrous and not or scarcely dilated below, branches 1.3–1.6 mm long, hispidulous. *Nutlet* shortly stipitate, stipe *c*. 0.4 mm long, somewhat constricted, obovoid to broad ellipsoid, obscurely trigonous, dull, mid-brown, 1.8–2.0 mm long including the stipe and style base, 1.0–1.3 mm diam., faces smooth, puberulous especially near apex, epidermal cells square–hexagonal, inconspicuous, with three fine white ribs, style base slightly enlarged, thick, persistent, cap-like, *c*. 0.2 mm long; embryo not examined. Photosynthetic pathway not examined. *2n* = unknown. (Figure 24).

Fig. 24. *Tricostularia newbeyi*. Western Australia. A. Habit. B, C. Inflorescence with stamens and old styles. D. Habit. E. Plant base. F. Inflorescences. Voucher: A–C: Starvation Boat Harbour, *G. Byrne 2545* (PERTH); D–F: Near Cocklebiddy, *M.D. Crisp 4775* (NSW). Photos A–C by G. Byrne; D–F by R.L. Barrett.

Diagnostic characters: Closely related to *T. compressa*, differing in the generally taller stature (0.2–0.9 m high), thicker culms with 1(2) nodes, longer inflorescences (1.5–6 cm long) with 6–9 nodes and acute glumes.

Distribution: Endemic to the south-west of Western Australia, from Albany east to Esperance and the Cocklebiddy area.

Habitat: Grows on flat sandplains, gentle slopes or dunes, in deep white, yellow, brown or grey sands, sometimes over clay in winter-wet areas or over laterite or limestone. Recorded in association with *Callitris* sp., *Eremaea* sp., mallee *Eucalyptus* spp., *E. incrassata*, *Gahnia deusta*, *G. lanigera*, *Lepidosperma fairallianum*, *L.* sp. Mount Ridley (K.L. Wilson 9247), *Mesomelaena stygia* ssp. *stygia*, *Morelotia microcarpa*, *Netrostylis* sp. Mt Madden (C.D. Turley 40 BP/897), *Schoenus caespititius* and *S. racemosus*.

Phenology: Flowers October–December.

Conservation status: Recorded as locally common and relatively widespread in a variety of habitats, so not considered threatened. Conserved in a number of conservation reserves including Stirling Range National Park, Cape Arid National Park, Nuytsland Nature Reserve and Dola Reserve. IUCN: Least Concern.

Specimens examined: WESTERN AUSTRALIA: Saddleback Hill, 2 Dec. 2009, *E. Adams & C. Turley EA 615* (PERTH); Plot 5110, Redmond State Forest, N of Hunwick Road, 6 Nov. 1991, *A.R. Annels ARA 1889* (PERTH); 7.2 km SW of Rawlinson Road on West Point Road, 12 Dec. 1983, *M.A. Burgman & C. Layman MAB 2893* (PERTH); 3.8 km N of the Starvation Boat Harbour camping area on Southern Ocean Road, 22 Nov. 2006, *G. Byrne 2545* (PERTH); 20 km SSW of Cocklebiddy along track to Twilight Cove, 4 Jan. 1979. *M.D. Crisp 4775* (CBG, NSW); side of North Woogenilup Road (Flora road), 4 Feb. 1997, *R. Davis 2493* (PERTH); 4.9 km E along Chillinup road from junction of Kojaneerup West Road, 19 Nov. 2013, *R. Davis & M. Davis RD 12395* (PERTH); Quadrat 1, Dolphin Cove Road Tank, Cape Arid National Park, 7 Oct. 2013, *D.J. Edinger & G. Marsh DJE 4094* (PERTH); Stirling Range National Park, survey site SWA0201D, 28 Oct. 2013, *R. Meissner, C. McCormack & M. Langley 6295* (PERTH); Stirling Range National Park, survey site SWA0203B, 31 Oct. 2013, *R. Meissner, C. McCormack & M. Langley 6296* (PERTH); 3.5 km SE of Chillinup Pool, 28 Nov. 1974, *K.R. Newbey 4619* (PERTH); Lot 14, View Range Road, [SE of] Tenterden, 29 Dec. 2007, *J.E. Wajon 1615* (PERTH); SRNP [Stirling Range National Park] C13, Murray site, 1.35 km S of North-East Track on North Isongorup Track. W from road, 8 Dec. 1988, *R.T. Wills 1410* (PERTH); Site SRNP C19, Murray Site, intersection of South Mirlpunda Track and Ellen Track, S from road, 9 Dec. 1988, *R.T. Wills 1411* (PERTH); 20 km S of Cocklebiddy on track to Twilight Cove, 3 Dec. 1994, *K.L. Wilson & K. Frank 9263* (NE, NSW, PERTH).

Etymology: Named in memory of Kenneth Raymond Newbey (1936–1988), a plant ecologist, botanical collector, horticulturalist and farmer from the Ongerup region who collected many new species from southern Western Australia and had a particular interest in Cyperaceae.

Common name: Newbey's Tricostularia.

Notes: While quite widespread, the resemblance of this species to *T. compressa* and presumed variation in that species meant it was overlooked until recent years.

Tricostularia pauciflora (F.Muell.) Benth., *Fl. Austral.* 7: 383 (1878).

Lepidosperma pauciflorum F.Muell., *Fragm.* 9: 23 (1875). *Schoenus pauciflorus* (F.Muell.) F.Muell., *Syst. Cens. Austral. Pl.* 1: 128 (1882).

Type citation: "In planitiebus uliginosis exsiccantibus prope Mount Abrupt, F. Mueller; prope Mount William, Sullivan."

Type: VICTORIA: prope [near] Mt Abrupt, November 1853, *F. Mueller s.n.* (lectotype (designated by Barrett and Wilson 2012: 287): MEL 2295903; isolecto: K 000960122, MEL 2295898, MEL 2295899, MEL 2295900, MEL 2295902).

Residual syntypes: near Mt William, 12 Nov. 1873, *D. Sullivan 14* (syn: K 000960123, MEL 2295901).

Cladium pauciflorum R.Br., *Prodr.* 237 (1810). *Chapelliera pauciflora* (R.Br.) Nees in J.G.C. Lehmann (ed.) *Pl. Preiss.* 2(2–3): 444 (1848). *Cladium junceum* var. *pauciflorum* (R.Br.) Kük., *Rep. Spec. Nov. Regni Veg.* 51: 182 (1942).

Type citation: "(J.) v.v."

Type: New South Wales: Port Jackson, 1 July 1802, *R. Brown* [*Bennett No. 6048*] (syn: BM 000798948, E 00303230*, K 000960124).

Illustrations: Metcalfe (1971; fig. 68a–c); Wilson (1993: fig. 57a–c); Morris (1994: figs 30L, 40).

Perennial tufted herb, 0.1–0.45(–70) m high; plants clonal, forming dense tussocks 0.1–0.3 m across; rhizome thin, woody, short, branched, 1–2 mm diam., non-pseudobulbous; old leaf sheaths covering the rhizome, not breaking apart into fine fibres with age, pale to reddish brown; roots sand-binding. *Culms* slender, rigid, erect, often arcuate, with 1(2) nodes or not noded, terete, not or scarcely grooved, 0.5–1.2 mm diam., smooth, glabrous, green to yellow-green, base somewhat tapering. *Leaves* mostly basal, numerous, and sometimes 1 or 2 cauline; phyllotaxy loosely spirotristichous; sheath 11–17 mm long, 0.7–1.5 mm wide, slightly broader

than the leaf lamina, margins glabrous, straw-coloured to dark red-brown, dull, upper margin membranous, oblique, glabrous, ligule absent; cauline sheath tight around culm; *pseudopetiole* obscure or absent; basal leaves often with a much reduced lamina, not exceeding the culms, lamina dorsiventral, 0.5–6(–7) cm long, 0.3–0.7 mm wide; bases not differentiated, not dividing; lamina ± linear, channelled, ± flexuous, old leaf tips not curling, finely multi-striate, margins glabrous or with a few minute scabrosities, otherwise glabrous, brown, concolorous, weakly keeled along mid-nerve, margins not recurved, apex long-attenuate, setaceous; lowest leaves reduced to a sheath, lacking a lamina, pale to reddish brown. *Inflorescence* contracted, panicle-like, narrow, ± obloid, somewhat flexuous, with 0 or 1(2) nodes, 0.8–1.5 cm long, 5–8 mm wide, usually not interrupted, axis green or yellow-green, not glaucous; bracts reduced leaf-like, not exceeding the spikelet clusters, sheaths open, not enveloping the higher bracts, gradually reducing along the inflorescence, basal bract somewhat shorter than inflorescence, to 12 mm long; branch(es) erect, margins scabrous, with solitary or 2 or 3 spikelets in a terminal cluster (rarely with a second distant cluster), spikelet(s) on short, terete, glabrous peduncles 1–3 mm long, arising in each bract axil; spikelet prophyll present, sheath 3–4.5 mm long, brown, with 3 distinct veins, partially enclosing the spikelet, with a slender lamina 0.6–1.0 mm long, brown. *Spikelets* brown, lanceolate, 4–6 mm long, terete, with 5 or 6 glumes, only topmost 2 or 3 fertile, the lower 1 or 2 flowers male, sterile or fertile, the upper flower bisexual, fertile, no reduced glume above the florets; glumes subdistichous, basal glume 2.5–3.5 mm long, fertile glumes 2.9–4.0 mm long, 1.5–2.8 mm wide, membranous, very pale red-brown to very dark red-brown (apex often darker than body), sparsely scabrous on the keel, lamina glabrous, ovate-lanceolate, acute to acuminate, with a mucro to 0.5 mm long, keel distinct; rachilla compact and not sinuous in fruiting spikelets. *Perianth segments* 6, whitish, minute, 0.2–0.8 mm long, expanded below, tapering to a fine point, glabrous, sometimes persistent but usually falling with nutlet. *Stamens* 3; anther connective 2.3–3.8 mm long, subulate; anthers cream, 1.4–1.6 mm long, with a glabrous apical appendage 0.15–0.2 mm long. *Style* trifid, base 0.5–1.2 mm long, glabrous, slender above, not or scarcely dilated below, branches 1.5–2.0 mm long, hispidulous. *Nutlet* shortly stipitate, stipe *c.* 0.5 mm long, somewhat constricted, obovoid to obpyriform or broad ellipsoid, obscurely trigonous, dull, mid-brown to dark brown, 2.1–2.5 mm long including the style base, 1.2–1.5 mm wide, faces smooth, puberulous especially near apex, epidermal cells square–hexagonal, inconspicuous, with three fine white ribs, style base only slightly enlarged, thick, persistent, very shortly conical; embryo not examined. Photosynthetic pathway inferred from anatomy to be C_3 (Takeda *et al.* 1985; *Willis s.n.*, 1 Oct 1959; *Briggs 3961*; Bruhl & Wilson 2007). (Figure 25).

Diagnostic characters: Distinguished from all other *Tricostularia* species by the highly reduced inflorescence with only 1–3 spikelets.

Distribution: South from Limeburners Creek Conservation Reserve in coastal New South Wales, extending inland to the Gibraltar Range and the Blue Mountains. Common in the Gippsland area, then apparently disjunct to Wilsons Promontory, extending west from there through Anglesea, Casterton and the Grampians, to Penola in South Australia. Isolated records in the southern Mount Lofty Ranges, and a single record from Kangaroo Island. Scattered in the north-east and east coast of Tasmania, including Cape Barren Island in the Furneaux group.

Habitat: Grows damp sandy heathlands, open *Eucalyptus* woodland, grasslands and dunes associated with sandstone or granite, mainly in near coastal areas.

Recorded in association with *Allocasuarina distyla*, *A. muelleriana*, *Amperea xiphoclada*, *Anthelepis paludosus*, *Aotus ericoides*, *Astroloma pinifolium*, *Austrostipa mollis*, *Banksia ericifolia*, *B. serrata*, *Burchardia umbellata*, *Caesia parviflora*, *Callitris rhomboidea*, *Calytrix alpestris*, *Caustis flexuosa*, *C. pentandra*, *Chaetospora turbinata*, *Corymbia gummifera*, *Epacris impressa*, *Eragrostis brownii*, *Eucalyptus baxteri*, *E. haemastoma*, *E. obliqua*, *E. pilularis*, *E. serraensis*, *Gahnia radula*, *G. sieberiana*, *Grevillea aquifolium*, *Hypolaena fastigiata*, *Isopogon ceratophyllus*, *Juncus continuus*, *J. planifolius*, *Laxmannia orientalis*, *Lepidosperma canescens*, *L. concavum*, *L. filiforme*, *L. semiteres*, *L. sieberi*, *Leptospermum attenuatum*, *L. myrsinoides*, *L. polygalifolium*, *L. scoparium*, *Lepyrodia scariosa*, *Lomandra longifolia*, *Lomatia ilicifolia*, *Machaerina acuta*, *Monotoca scoparia*, *Patersonia fragilis*, *Petrophile pulchella*, *Platylobium obtusangulum*, *Poa morrisii*, *Prostanthera saxicola*, *Ptilothrix deusta*, *Schoenus apogon*, *S. brevifolius*, *S. imberbis*, *S. pachylepis*, *Styphelia adscendens*, and *Xanthorrhoea australis*.

Phenology: Flowers recorded for August–December.

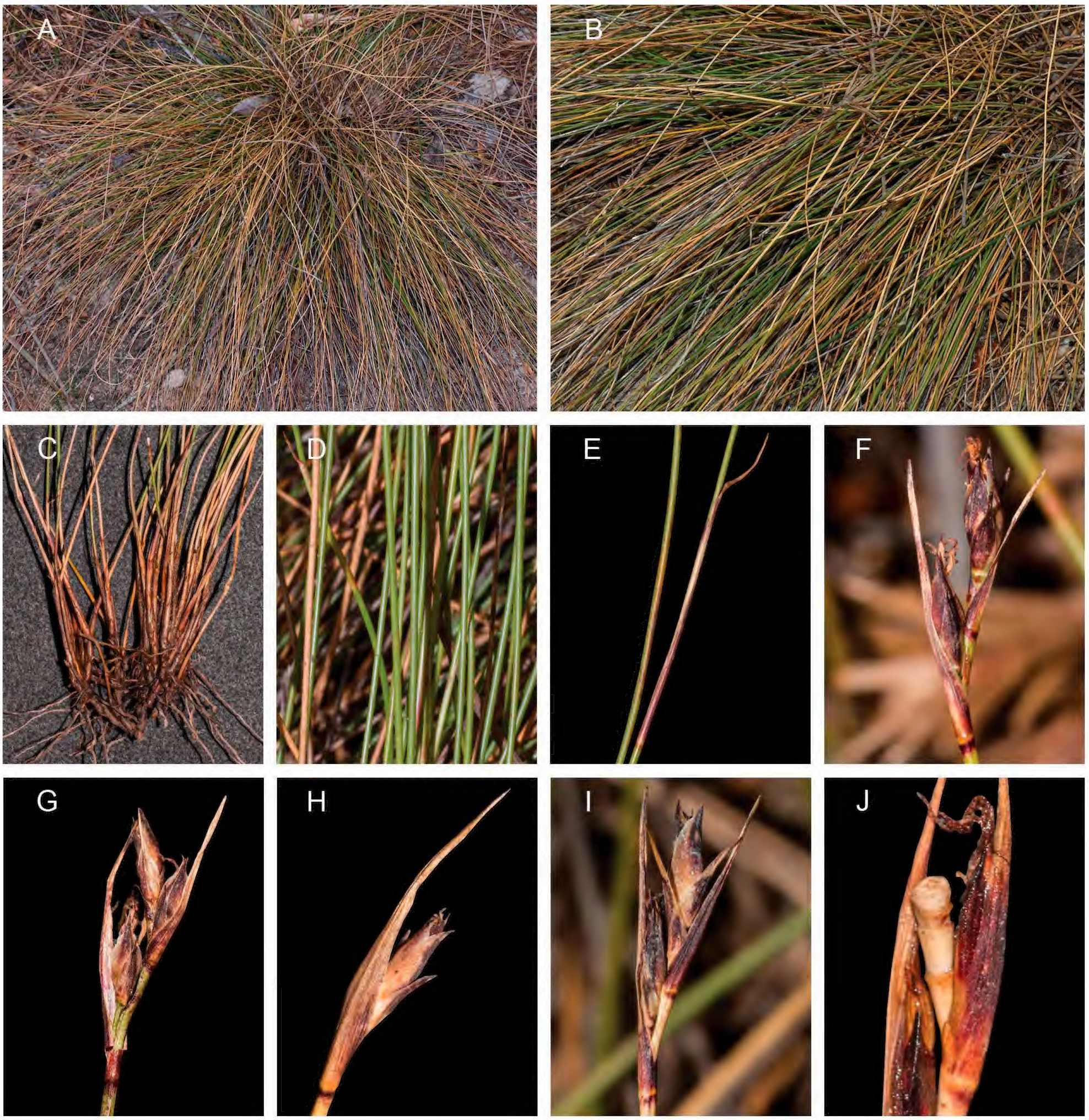

Fig. 25. *Tricostularia pauciflora*. Royal National Park, New South Wales. A, B. Habit. C. Plant base. D. Culms. E. Leaf sheath and reduced lamina. F–I. Inflorescence. J. Rachilla with glumes fallen and persistent inflorescence bract. Voucher: *R.L. Barrett 9313* (NSW); Photos by R.L. Barrett.

Conservation status: Widespread and not threatened as a species. Uncommon east of Port Phillip Bay in Victoria (Wilson 1993). Probably common and widespread throughout the southern Mt Lofty Ranges in South Australia before settlement, but now much reduced (Jessop and Weber 1986). Apparently rare in Tasmania (Morris 1994). IUCN: Least Concern.

Specimens examined: SOUTH AUSTRALIA: Yallum [?Park], 9 miles W of Penola, 15 Dec. 1963, *A.C. Beauglehole ACB 5911* (AD, *n.v.*, MEL); Comaum Nature Forest Reserve, Alcock's Scrub, EW track off NS track adjacent pine plantation, 14 Feb. 2006, *D.J. Duval 390* (AD, *n.v.*, MEL). NEW SOUTH WALES: Mowlee Ridge, E of Bundeena road on Little Marley Track, Royal National Park, 15 Sept. 2020, *R.L. Barrett 9313* (NSW); Manly, Oct. 1894, *E. Betche s.n.* (NSW 687702); Morton National Park, off track to Tianjara Falls carpark, N of Nerriga (Turpentine) Rd, 31 Dec. 2008, *J.J. Bruhl & F.C. Quinn 2701* (BOL, BRI, CANB, EIU, K, NE, NSW); near western boundary of Gibraltar Range National Park, park along Gwydir Highway between Glen Innes and Grafton, 21 Oct. 1988, *S. Krauss 113* (NSW); Ku-ring-gai Chase National Park, Dark Hole track, 25 Apr. 2009, *P.M. Musili, J.J.Bruhl & K.L. Wilson 534A* (BRI, EA, K, NE, NSW, PERTH); Topham Track, W of West Head Road, Ku-ring-gai Chase National Park, 28 Nov. 1990, *K.L. Wilson 7654* (K, NSW, P); Mowlee Ridge, E of Bundeena road on Little Marley Track, Royal National Park, 28 Nov. 2012, *K.L. Wilson & O. Yano 10941* (NE, NSW). VICTORIA: on E side of Grampians Tourist Road, *c.* 29 km S. of Halls Gap, Grampians

National Park, 5 Oct. 2008, *R.L. Barrett RLB 5222* (PERTH); 7 miles [12 km] E of Vic./S.A. border, N side of Dergholm–Penola road, 9 Nov. 1964, *A.C. Beauglehole ACB 16333* (AD, CANB, LTB, *n.v.*, MEL, NE, NSW); lower western slopes of Mt Abrupt, by roadside N of walking track to summit, 28 Oct. 1995, *I.C. Clarke 2615* (CANB, MEL); SE of Portland, Alcoa smelter site, 1.1 km SW of Blacknose Point, 18 Nov. 1980, *M.D. Crisp 6900* (CBG, NSW); 1.2 km from Knights Bridge over the Wannon River, Dunkeld-Halls Gap Road, roadside verge, E side, 29 Dec. 2008, *A.K. Gibbs & A.R. Fitzpatrick 88* (BRI, K, MEL, NE, NSW); Anglesea, Shining Eye Track. Grid P 20, 22 Dec. 1990, *V. Stajsic 110* (HO, *n.v.*, MEL, NSW); Black Rock, Royal Melbourne Golf Club, 15 Dec. 2016, *V. Stajsic, S.J. Moodie & J. Stewart 8322* (NE, MEL). TASMANIA: Waldheim, 27 Jan. 1962, *M.E. Phillips 461* (CBG); *c.* 2 km NW of Coles Bay on Bicheno road, 21 Feb. 1986, *K.L. Wilson 6517* (HO, NSW).

Etymology: From the Latin *pauci-* (few) and *-florus* (flowered).

Common name: Needle bog-rush.

Notes: This is the only species in the genus in south-eastern Australia. There are some particularly small forms in Victoria that warrant further study.

Cladium pauciflorum R.Br. (Brown 1810) was published well before *Lepidosperma pauciflorum* F.Muell. (Mueller 1875), the two names were regularly treated as belonging to discrete taxa and often placed in separate genera (e.g. Mueller (1875: 16) where Brown's name was treated as a synonym of *Cladium junceum* R.Br. (=*Machaerina juncea* (R.Br) T.Koyama)). Bentham (1878) combined Mueller's name in *Tricostularia*, while treating Brown's name as a probable variety of *Cladium junceum*. Brown's name therefore cannot be transferred to *Tricostularia* as it would be a later homonym.

Tricostularia sandifordiana R.L.Barrett & K.L.Wilson, *sp. nov*.

Type: Western Australia: access track to Granite Hill Nature Reserve, 1.4 km E of Moorialup Road at junction of minor track, 16 Nov. 2003, *M. Hislop 3092* (holo: NSW; iso: PERTH 06701809).

Tricostularia sp. South Coast (R.T. Wills 1423), *FloraBase* (2008–), accessed 4 June 2020.

Perennial herb, 0.3–0.9 m high; plants clonal, 0.5–2 m across, culms widely spaced along rhizomes; rhizome thin, woody, very long, branched, 0.8–1.8 mm diam., not pseudobulbous; old leaf sheaths covering the rhizome, partly breaking apart into fibres with age, straw-coloured or pale brown; roots sand-binding. *Culms* slender, rigid, erect, with 2–5 nodes, ± terete, sometimes drying irregularly angular, very finely striate, 0.7–1.7 mm diam., smooth, glabrous, bright green to yellow-green, base not enlarged. *Leaves* greatly reduced, 2–5, cauline; phyllotaxy loosely spirotristichous; sheath 9–21 mm long, 1.7–3.3 mm wide, flared open at the apex and broader than the leaf lamina, margins glabrous, brown to dark red-brown, dull, upper margin somewhat membranous, prominently auriculate, oblique, glabrous, ligule absent; sheath tight around culm; *pseudopetiole* obscure or absent; cauline leaves with a much reduced lamina, not exceeding the culms, lamina dorsiventral, 0.6–1.1 cm long, 0.6–0.9 mm wide; bases not differentiated, not dividing; lamina ± linear, channelled, ± flexuous, old leaf tips not curling, finely multi-striate, margins finely scabrid, otherwise glabrous, green, concolorous, not keeled along mid-nerve, with 3 fine impressed nerves, margins ribbed and finely scabrous, not recurved, apex long-attenuate, acute; lowest leaves reduced to a sheath and lacking a lamina or with a short lamina to 3.5 mm long, straw-coloured or pale brown. *Inflorescence* contracted, panicle-like, narrow, not flexuous, with 0 or 1 nodes, 1.7–4.5 cm long, 10–17 mm wide, commonly interrupted, axis green or yellow-green, not glaucous; bracts reduced leaf-like, not exceeding the spikelet clusters, sheaths open, not enveloping the higher bracts, gradually reducing along the inflorescence, basal bract shorter than inflorescence, 17.1–18.8 mm long; branches erect, with 2–5 spikelets per cluster in a terminal or two distant clusters, spikelet(s) on short, slightly compressed, glabrous peduncles 1–3.5 mm long, arising in each bract axil; basal branch 8–12 mm long; spikelet prophyll present, broad, sheath 6.8–8.2 mm long, apex auriculate, brown, with raised keel, partially enclosing the spikelet, with a slender lamina 0.8–2.4 mm long, brown or green. *Spikelets* brown, lanceolate, 8–10 mm long, 1.4–2.0 mm wide, compressed, with 7 developed glumes and two highly reduced basal glumes, only topmost 2 fertile, the lower flower male fertile, the upper flower bisexual, fertile, no reduced glume above the florets; glumes distichous, reduced basal glumes 1.6–2.1 mm long, translucent, lowest developed glume 3.6–3.9 mm long, fertile glumes 6.3–9.8 mm long, 1.5–2.8 mm wide, membranous, straw-coloured to very pale red-brown (apex often darker than body), finely scabrous on the keel and sometimes on the upper margins, otherwise glabrous, ovate-lanceolate, acute, sometimes with a mucro to 0.5 mm long, keel distinct; rachilla compact and not or scarcely sinuous in fruiting spikelets. *Perianth segments* 6, whitish, minute, *c.* 0.6 mm long, expanded below, tapering to a fine point. *Stamens* 3; anther connective 3.1–3.6 mm long, subulate; anthers yellow, 4.2–4.6 mm long, with a glabrous apical appendage up to 0.9 mm long. *Style* trifid, base 2.3–3.2 mm long, hispidulous and slender above, scarcely dilated below, branches 2.1–2.9 mm long, hispidulous. *Nutlet* [not seen fully mature] shortly stipitate, stipe *c.* 0.3 mm long, somewhat constricted, narrowly ovoid, obscurely trigonous, dull, mid-brown, 1.7–2.1 mm long including the stipe and style base, 0.8–1.1 mm diam., faces

smooth, glabrous, apex smooth, glabrous, epidermal cells ovate–hexagonal, inconspicuous, with three fine white ribs, style base only slightly enlarged, thin, persistent, cap-like; embryo not examined. Photosynthetic pathway not examined. (Figure 26).

Fig. 26. *Tricostularia sandifordiana*. A. Habitat. B. Habit. C. Plant base. D. Inflorescences (two left) and cauline leaf with flared sheath apex (right). E. Immature nutlet with staminal filaments and style attached. Western Australia. Voucher: *R.T. Wills 1423* (PERTH). Images A, B by K.L. Wilson; C, D by A. Curtis; E by R. Davis.

Diagnostic characters: The widely spreading rhizomes bearing distant culms and broadly flared leaf sheaths and inflorescence bracts are not shared by any other *Tricostularia* species.

Distribution: Endemic to the south-west of Western Australia, between Albany and the Stirling Range.

Habitat: Grows in low heath and *Banksia coccinea* shrubland (Sandiford and Barrett 2010), on winter-wet white or grey sands on plains or gentle slopes, sometimes along drainage lines. Recorded in association with *Adenanthos cuneatus*, *A. obovatus*, *Agonis theiformis*, *Allocasuarina decussata*, *A. fraseriana*, *Anarthria gracilis*, *A. prolifera*, *A. scabra*, *Andersonia micrantha*, *A. pinaster*, *Banksia attenuata*, *B. baxteri*, *coccinea*, *B. grandis*, *B. ilicifolia*, *B. nutans*, *Callistemon glaucus*, *Calytrix flavescens*, *Caustis dioica*, *Chaetospora curvifolia*, *Conospermum caeruleum*, *Conostylis serrulata*, *Corymbia calophylla*, *Cyathochaeta avenacea*, *C. clandestina*, *C. equitans*, *Dasypogon bromeliifolius*, *Eucalyptus cornuta*, *E. marginata*, *E. staeri*, *Harperia confertospicata*, *Hypocalymma strictum*, *Hypolaena exsulca*, *Jacksonia spinosa*, *Johnsonia* sp., *Kunzea ericifolia*, *Lepidosperma drummondii*, *L.* aff. *squamatum*, *L.* sp. Torndirrup (B. Muir 73), *Leptocarpus tenax*, *Leucopogon elegans*, *L. flavescens*, *L. glabellus*, *Lyginia barbata*, *Lysinema ciliatum*, *Melaleuca striata*, *M. thymoides*, *Mesomelaena tetragona*, *Pericalymma ellipticum*, *Petrophile rigida*, *Phlebocarya ciliata*, *Phyllota barbata*, *Pimelea longifolia*, *Platysace pendula*, *Schoenus caespititius*, *S. efoliatus*, *S. sublateralis*, *Stylidium scandens*, *Taxandria angustifolia*, *T. parvifolia*, *Tremulina tremuloides*, *Tricostularia drummondii* and *Xanthosia rotundifolia*.

Phenology: Flowers recorded for November–December. Immature fruit present in December.

Conservation status: The twelve collections are from nine locations between Redmond (north of Albany) and Isongorup Peak in the Stirling Range. While plants are locally relatively common, population size is probably relatively small due to the extensive clonal nature of this species. One population is known from Phillips Brook Nature Reserve and two from the Stirling Range National Park, while four are on private property and two are in roadside remnants.

Specimens examined: WESTERN AUSTRALIA: Phillips Brook Nature Reserve (on W side of Albany Highway, entrance opposite Millbrook Road), NW of Albany, 22 May 2008, *R.L. Barrett & B.R. Gaskell RLB 5045* (PERTH); SW corner of Bloxidge Road and Pfeiffer Road, South Stirling (*c.* 22 km N of South Coast Hwy from Manypeaks Store), 22 May 2008, *R.L. Barrett RLB 5046* (PERTH); Millbrook Road, 4.0 km E of Albany Highway, in valley above estuary, 28 Oct. 2008, *R.L. Barrett & K.L. Wilson RLB 5360* (PERTH); 1.2 km W of junction of Chokerup Siding Road and Chokerup Road, Walpole Region, 10 Mar. 1997, *N. Casson & K. Kershaw W 169.17* (PERTH); bushland remnant, SE corner Plantagenet Loc 5873, Palmdale Road, South Stirling Plains, 5 Nov. 2002, *E.M. Sandiford EMS 659* (PERTH); remnant vegetation, Plantagenet Loc 6144, Woogenilup North Road, S of the Stirling Ranges, 9 Nov. 2002, *E.M. Sandiford EMS 672* (PERTH); remnant vegetation, Plantagenet Loc. 5951, ITC Gunnamatta Tree Farm, Johnson Road, N of Manypeaks, 10 June 2003, *E.M. Sandiford EMS 793* (PERTH, NSW); remnant vegetation Plantagenet Loc 5193, ITC Chorkerup Tree Farm, Chorkerup Road, Chorkerup Siding, 8 Aug. 2003, *E.M. Sandiford EMS 851* (PERTH); northern end of South Talyuberlup Track, Stirling Range National Park, 11 Nov. 2004, *E.M. Sandiford EMS 987* (PERTH); Phillips Brook Nature Reserve, Albany Hwy, NW of Albany, 8 Nov. 2007, *E.M. Sandiford 1350* (PERTH); Site SRNP [Stirling Range National Park] C13, Murray site, 1.35 km S of North-East Track on North Isongorup Track, W from road, 8 Dec. 1988, *R.T. Wills 1423* (PERTH); Millbrook Nature Reserve, *c.* 450 m along track S of NW corner of reserve, 26 Nov. 1994, *K.L. Wilson & K. Frank 9072* (NSW); Millbrook Nature Reserve, just inside NW corner of reserve, 26 Nov. 1994, *K.L. Wilson & K. Frank 9082* (NSW); 0.5 km N of Redmond–Hay River Road on Chorkerup Road, 26 Nov. 1994, *K.L. Wilson & K. Frank 9087* (NSW); 0.4 km N of Redmond intersection on Chorkerup Siding road, 10 May 1995, *K.L. Wilson 9349* (NSW).

Etymology: Named in honour of Elizabeth (Libby) M. Sandiford and her work in documenting plant diversity in southern Western Australia, particularly in the Albany region (e.g. Sandiford and Barrett 2010; Wilkins and Sandiford 2020). The name is also a play on the common habitat of this species in sandy, seasonally wet areas, 'ford' being a water-crossing.

Common name: Sandiford's Tricostularia.

Notes: The plant habit has a remarkable resemblance to some species of Restionaceae due to the multi-noded culms with large, flared bracts. The erect culms that are widely spaced on the rhizome also give a distinctive appearance similar to a number of south-west Australian species of Restionaceae. Several collections have been determined as Restionaceae sp. in the field, and one collection was even sent to Restionaceae expert Barbara Briggs for determination. The flared apex of the bracts is particularly similar in appearance to those of *Lepidobolus* Nees, and the compact inflorescence is also not dissimilar.

Noted to resprout and able to develop fertile growth within two years following fire.

Tricostularia sp. Albany (R.L. Barrett & K.L. Wilson RLB 5342)

Diagnostic characters: Similar to *T. drummondii* and *T. exsul*, differing in the intermediate inflorescence length, 5–8 cm long (3–4 cm long for *T. drummondii*; 8–12 cm long for *T. exsul*). (Figure 27).

Distribution: Endemic to the south-west of Western Australia, along the south coast between Scott River and Fitzgerald River.

Habitat: Grows in a variety of soils, from deep white or grey sands in winter wet depressions, sand over laterite, brown sandy clay over clay-granite, or dark brown loam, on plains or gentle slopes. Recorded in association with *Allocasuarina humilis*, *Anarthria scabra*, *Aphelia brizula*, *Banksia formosa*, *Baxteria australis*, *Beaufortia decussata*, *Centrolepis strigosa*, *Chaetospora subbulbosa*, *Corymbia calophylla*, *Eucalyptus marginata*, *Evandra aristata*, *Lepidosperma drummondii*, *L.* cf. *pubisquameum*, *Melaleuca thymoides*, *Phyllangium paradoxum*, Restionaceae, *Schoenus acuminatus*, *S. caespititius*, *S. discifer*, *S. lanatus*, *S. obtusifolius*, *S. racemosus*, *S. rodwayanus*, *S. sublateralis*, *S.* sp. Grey Rhizome (K.L. Wilson 2922) and *Tricostularia exsul*.

Phenology: Flowers recorded for September–October.

Conservation status: Relatively widespread and locally common. IUCN: Least Concern.

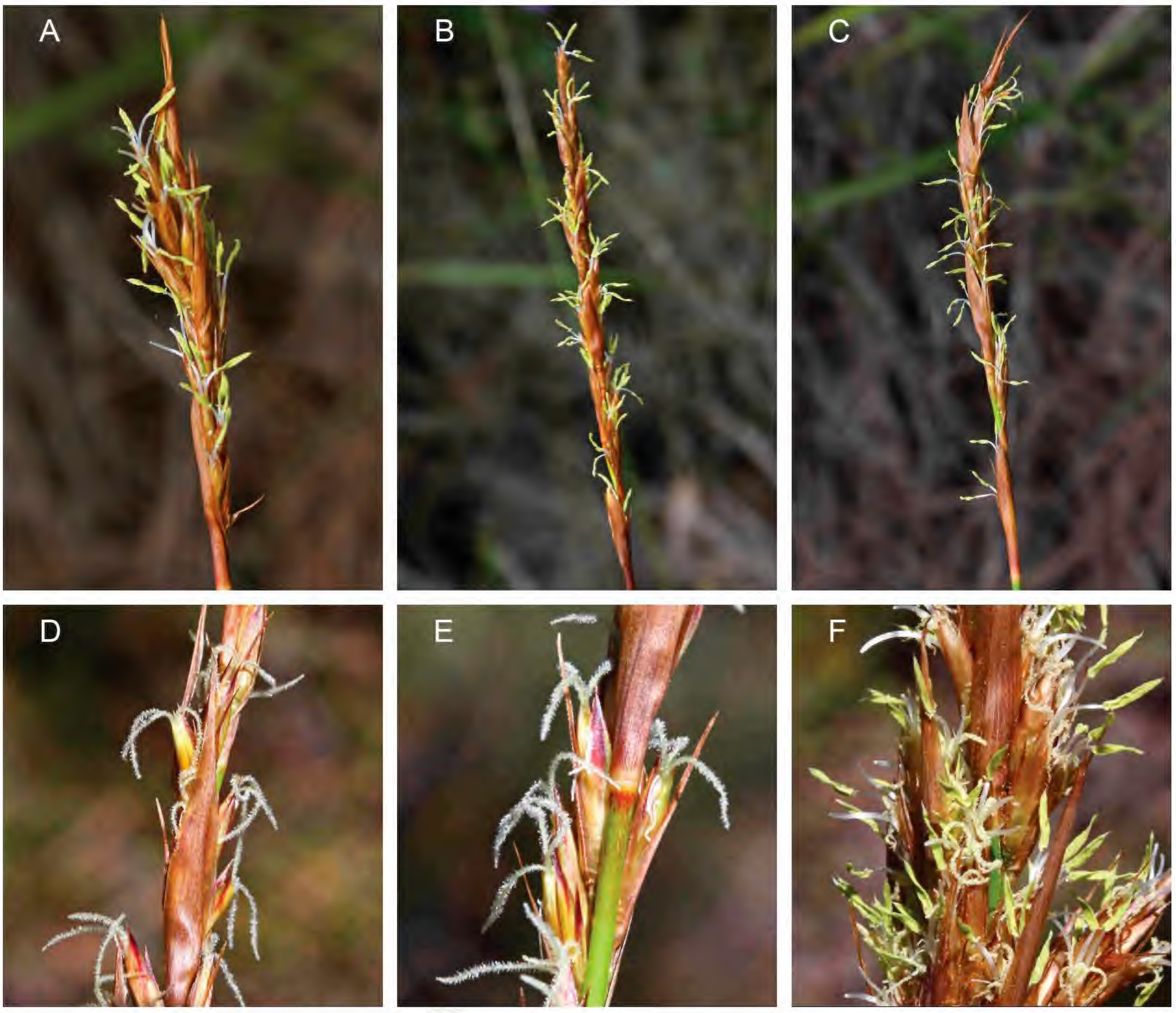

Fig. 27. *Tricostularia* sp. Albany (R.L. Barrett & K.L. Wilson RLB 5342). Bayonet Head, Western Australia. A–C. Full inflorescence with fresh stamens and a few styles. D, E. Spikelets with fresh styles. F. Spikelets with fresh anthers and a few styles. Voucher: *G. Byrne 4509* (PERTH). Photos by G. Byrne.

Specimens examined: WESTERN AUSTRALIA: Albany, 5 Jan. 1903, *C.R.P. Andrews 1153* (K, PERTH [as *s.n.*]); near corner of Roe and Western road, Manjimup, 7 Mar. 1990, *A.R. Annels 1113* (PERTH); Plot 5150, in Scout Reserve, 6.5 km SE of Mt Barker, 21 Sept. 1993, *A.R. Annels 3765* (PERTH); *c.* 1 km N on Gairdner South Road from Borden Bremer Bay Rd, W of Bremer Bay townsite, 7 Feb. 2008, *R.L. Barrett, M. Moody & N. McQuoid RLB 4389* (PERTH); *c.* 300 m down sand track from Albany Speedway, on S side of Albany Highway, 28 Oct. 2008, *R.L. Barrett & K.L. Wilson RLB 5342* (PERTH); Bushland NW of Lower King Road, Bayonet Head, 1 Dec. 2012, *G. Byrne 4509* (PERTH); Fitzgerald River National Park, 200 m W of Hamersley Drive on Hamersley Inlet Road, 20 Jan. 2010, *G.F. Craig 8682* (PERTH); 9 km ENE of Wellstead, 21 Jan. 1997, *R. Davis 2135* (PERTH); Nornalup Road, 23 km S of Mount Barker-Manjimup road, 21 Jan. 1998, *R. Davis 4869* (PERTH); 3 km NE of Bitter Water Swamp, Fitzgerald River National Park, 11 Nov. 1973, *K.R. Newbey 3997* (PERTH); 17 km N of Cape Riche, 30 Nov. 1975, *K.R. Newbey 4935* (PERTH); Lower King River, 1 Feb. 1993, *L.J. Pen LJP 304* (PERTH); Scott River Road, *c.* 4 km W of intersection with Milyeannup Coast Road, Scott National Park, 20 Nov. 1994, *K.L. Wilson 8973* (NSW, PERTH); Millbrook Nature Reserve, *c.* 600 m S along track from NW corner of reserve, 26 Nov. 1994, *K.L. Wilson 9077* (NE, NSW, PERTH).

Notes: Known to co-occur with *T. exsul*, and clearly distinct from that species, but the relationships between *T. exsul*, *T.* sp. Albany and *T. drummondii* would benefit from further clarification. Morphological variation in *T. drummondii* in particular is poorly understood, but molecular data suggest that all three taxa represent distinct lineages (Figure 3).

Tricostularia sp. Mogumber (A. Harris s.n., 23/12/2015)

Diagnostic characters: Superficially similar to *T. davisii*, but probably more closely allied to *T. neesii*, distinctive for its tall culms and sub-capitate heads. (Figure 28).

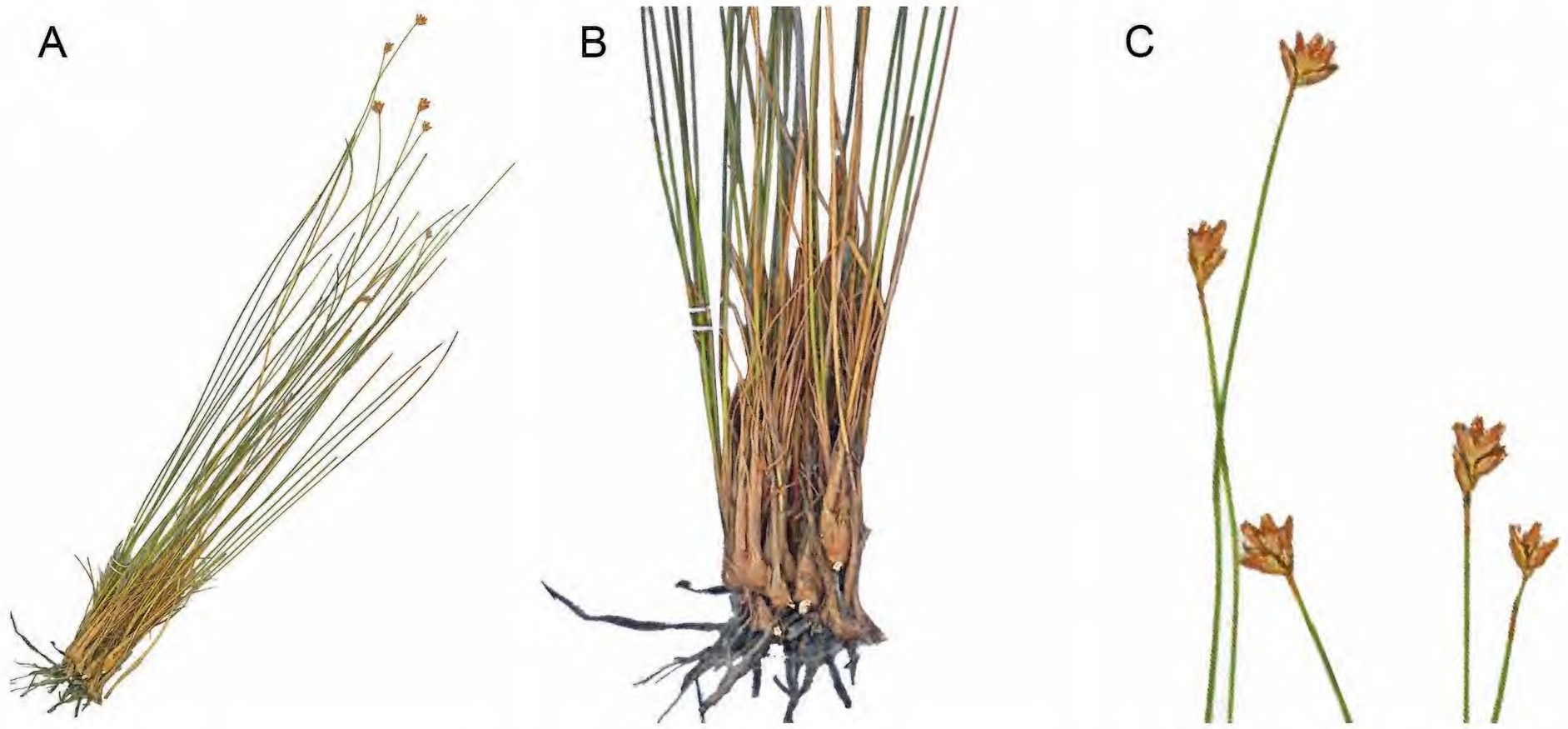

Fig. 28. *Tricostularia* sp. Mogumber (A.J. Harris s.n.; 23/12/2005). Near Mogumber, Western Australia. A. Habit. B. Plant base. C. Inflorescences. Voucher: *A.J. Harris s.n.*; 23 Dec. 2005). Images by A. Harris.

Distribution: Endemic to the south-west of Western Australia, between Mogumber and Lesueur National Park.

Habitat: Grows in low heath or open *Banksia* woodland on white or grey sand. Recorded in association with *Adenanthos cygnorum*, *Alexgeorgea nitens*, *Allocasuarina humilis*, *Banksia attenuata*, *B. dallanneyi* subsp. *pollosta*, *B. mimica*, *B. polycephala*, *Caustis dioica*, *Daviesia physodes*, *Desmocladus virgatus*, *Eucalyptus todtiana*, *Gastrolobium capitatum*, *Harperia lateriflora*, *Hibbertia subvaginata*, *Jacksonia floribunda*, *Lambertia multiflora*, *Lyginia barbata*, *Mesomelaena pseudostygia*, *Nuytsia floribunda*, *Patersonia occidentalis*, *Petrophile divaricata*, *Podotheca angustifolia*, *P. gnaphalioides*, *Scholtzia involucrata* and *Synaphea spinulosa*.

Phenology: Flowers probably in spring.

Conservation status: Poorly known and further conservation assessments are required. IUCN: Data Deficient.

Specimens examined: WESTERN AUSTRALIA: Lesueur National Park, Peron slopes on access firebreaks, Hill River 1:100,000 Grid. ref. 205677, Jan. 1993, *B. Evans 459* (PERTH); near Mogumber, 23 Dec. 2015, *A. Harris s.n.* (PERTH*).

Notes: Previously overlooked and confused with *T. neesii* which is probably the closest relative, differing in inflorescence structure. Further collections are required to assess the status of this taxon.

Tricostularia sp. Porongurup (I. Abbott 18)

Diagnostic characters: The twisted culms and large spikelets (7–9 mm long) are very distinctive. (Figure 29).

Distribution: Endemic to the south-west of Western Australia, known only from a single collection on the south side of the Porongurup Range.

Habitat: Grows in woodland over dense heath. Recorded in association with *Acacia drummondii* subsp. *elegans*, *Agonis theiformis*, *Anarthria laevis*, *Andersonia caerulea*, *Apium prostratum* subsp. *phillipii*, *Astartea scoparia*, *Banksia grandis*, *Beaufortia empetrifolia*, *Boronia crenulata*, *Bossiaea linophylla*, *Chaetospora subbulbosa*, *Darwinia citriodora*, *D. vestita*, *Desmocladus fasciculatus*, *Eutaxia myrtifolia*, *Evandra aristata*, *Kingia australis*, *Kunzea micrantha*, *Leptospermum spinescens*, *Lepyrdia monoica*, *Leucopogon glabellus*, *L. interstans*, *Lysinema pentapetalum*, *Melaleuca blaeriifolia*, *Mesomelaena tetragona*, *Microlaena stipoides*, *Mirbelia dilatata*, *Petrophile teretifolia*, Restionaceae, *Sonchus hydrophyllus*, *Stylidium crassifolium*, *Taxandria angustifolia*, *T. conspicua*, *T. linearifolia*, *Tremandra stelligera* and *Xanthosia rotundifolia*.

Phenology: Flowers not recorded, probably October–November.

Conservation status: The single known collection suggests this species may be localised, or it may simply have been overlooked. The collection was made on private land just south of the Porongurup National Park. IUCN Data Deficient.

Specimen examined: WESTERN AUSTRALIA: South side of Porongurup Range, Mira Flores Estate, Sept. 1975, *I. Abbott 18* (PERTH).

Fig. 29. *Tricostularia* sp. Porongurup (I. Abbott 18). Porongurup South, Western Australia. Voucher: *I. Abbott 18* (PERTH). Photos by R.L. Barrett.

Notes: Efforts to relocate the taxon at the original site by the first author have proven unsuccessful to date; however, the vegetation is largely intact, so it should still be present. It may be more obvious following fire as the vegetative ground cover was very dense at the time the survey to relocate the taxon was conducted.

Morphologically similar to *T. aphylla*, but markedly disjunct and easily distinguished by the more slender culms and larger spikelets.

Tricostularia sp. Two Peoples Bay (G. Wardell-Johnson GWJ 114)

Diagnostic characters: Similar to *T. exsul*, differing in the more slender culms (0.6–1 mm diam.) and the spikelets that are distant on the inflorescence axis and so usually do not overlap. (Figure 30).

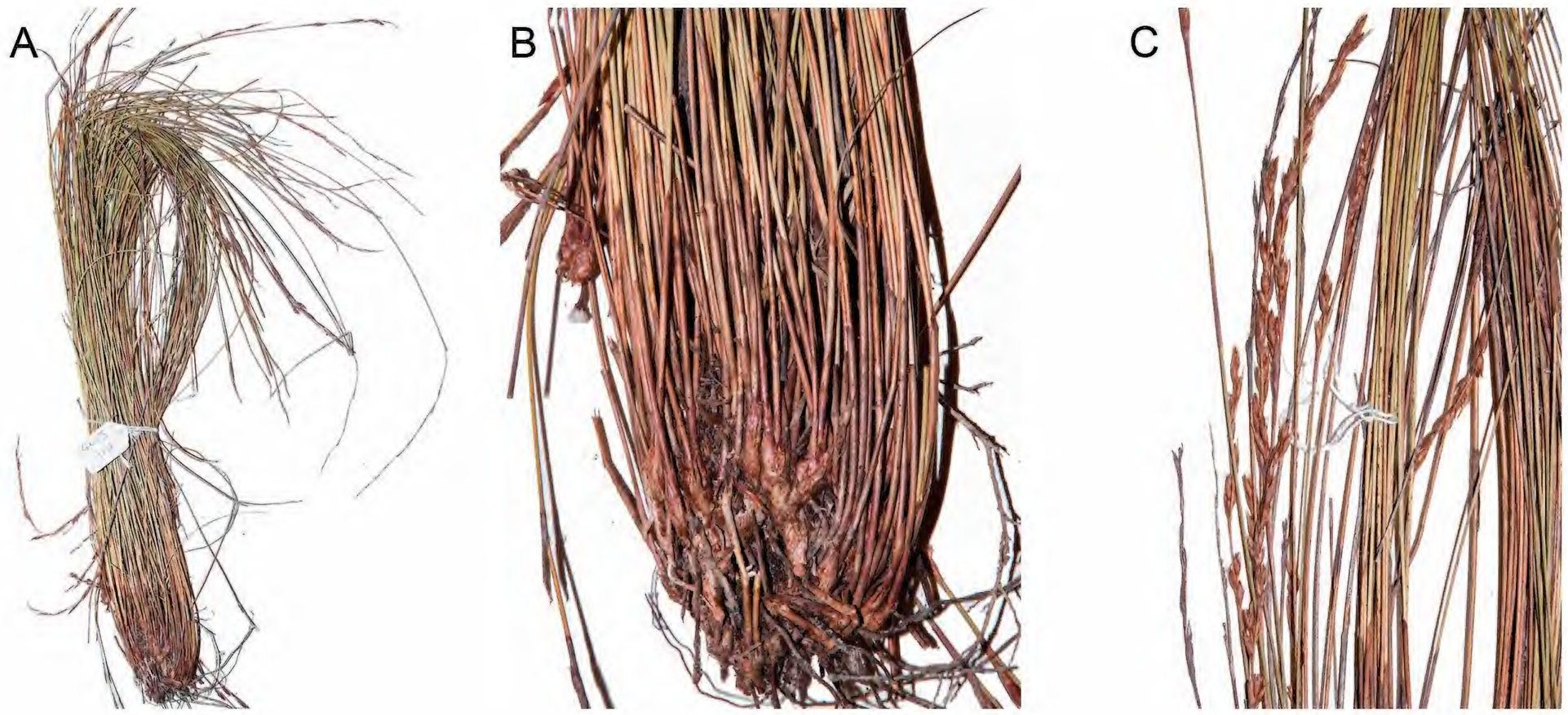

Fig. 30. *Tricostularia* sp. Two Peoples Bay (G. Wardell-Johnson GWJ 114). A. Habit at Two Peoples Bay, Western Australia. Voucher: *G. Wardell-Johnson GWJ 114* (NSW). Photos by R.L. Barrett.

Distribution: Endemic to the south-west of Western Australia and only known from two locations, near Two Peoples Bay, east of Albany, and near Bremer Bay.

Habitat: Grows in sand amongst granite boulders on a slope and on exposed plains in well-drained deep white sand. Recorded in association with *Acacia browniana*, *A. leioderma*, *A. robiniae*, *Agonis theiformis*, *Allocasuarina humilis*, *Anarthria gracilis*, *A. prolifera*, *A. scabra*, *Banksia formosa*, *B. gardneri*, *B. mucronulata*, *B. nutans*, *Boronia crenulata*, *B. spathulata*, *Conospermum caeruleum*, *C. teretifolium*, *Corymbia ficifolia*, *Crowea angustifolia*, *Daviesia incrassata*, *Gastrolobium coriaceum*, *Grevillea pulchella*, *Hakea ceratophylla*,

Jacksonia spinosa, *Lepidosperma drummondii*, *L. leptostachyum*, *Lepyrodia hermaphrodita*, *Leucopogon elegans*, *L. obovatus*, *L. verticillatus*, *Lomandra nigricans*, *L. pauciflora*, *L. sonderi*, *Lyginia barbata*, *Lysinema pentapetalum*, *Melaleuca diosmifolia*, *M. thymoides*, *Morelotia octandra*, *Patersonia umbrosa*, *Petrophile divaricata*, *P. diversifolia*, *Phlebocarya ciliata*, *Schoenus caespititius*, *S. sublateralis*, *Stirlingia tenuifolia* and *Xanthosia rotundifolia*.

Phenology: Flowers probably in spring.

Conservation status: Poorly known and further surveys are required. IUCN Data Deficient.

Specimens examined: WESTERN AUSTRALIA: 2.5 km NNE of Toolalup Swamp (Bremer Bay area), 3 Dec. 1975, *K.R. Newbey 4633* (NSW, PERTH); Plot 5455, W of Bettys Beach on Two Peoples Bay, Boulder Hill, 2 May 1992, *G. Wardell-Johnson GWJ 114* (NSW, PERTH).

Notes: Previously confused with *T. exsul*. Possibly just an extreme form of *T.* sp. Albany (R.L. Barrett & K.L. Wilson RLB 5342), but further fieldwork is required to determine the extent of variation in both taxa.

Xyroschoenus Larridon, *Mol. Phyl. Evol.* 127: 207 (2018).

Type species: *Xyroschoenus hornei* (C.B.Clarke) Larridon.

Perennial tufted *herbs*, 0.9–1.5(–2) m high; plants clonal, 0.3–1 m across; rhizome thick, woody, short, branched, 20–50 mm diam., not pseudobulbous, ultimately forming an erect caudex; old leaf sheaths covering the rhizome, sometimes breaking apart into fibres with age, reddish brown to dark brown; roots not sand-binding. *Culms* (above rosette) stout, erect, with 5–10 leafy nodes, obtusely trigonous, 3–9 mm diam., green, smooth, glabrous, base not enlarged. *Leaves* mostly basal, numerous, and 5–10 cauline; phyllotaxy loosely spirotristichous, sheath glabrous, open, 30–60 mm long, 20–30 mm wide, broader than the leaf lamina, brown, upper margin not membranous, ligule absent; basal leaves 50–90 cm long, (5–)10–15 mm wide, lamina dorsiventral, ± linear, coriaceous, curved, finely multi-striate, scabrid below on acute midrib, yellow-green, green, or sometimes dark green, slightly paler below, margins harshly scabrous to denticulate, sometimes splitting into fibres with age, revolute with age, apex gradually attenuate; cauline leaf lamina 20–50 cm long. *Inflorescence* open, panicle-like, spreading, lanceolate to ovate, 45–60 cm long, 10–55 cm wide, with 8–12 fertile nodes; axis green; bracts leaf-like, coriaceous, smooth, with reddish brown sheaths 20–25 mm long, becoming progressively smaller up the culm, shorter than the branchlets, basal bract usually much shorter than inflorescence; branchlets numerous, 8–25 cm long, arcuate downwards, solitary in lower part of inflorescence, the upper ones in groups of 4 or 5, arising in each bract axil, greatly exceeding the bract sheath; spikelets solitary on peduncles 3–8 mm long; spikelet prophyll subtending each spikelet glume-like, sheath 1.5–2.2 mm long, brown, partially enclosing the spikelet, with a slender lamina 3.1–4.5 mm long, brown. *Spikelets* very numerous, brown to dark brown, oblate to lanceolate, 5–8 mm long, 1.5–2 mm diam., acute, pendant to spreading, subterete, not compressed, with 7–9 glumes, the upper 2 larger glumes each subtending a flower, lower flower male, sterile, upper bisexual, fertile, lower 5–7 glumes empty, glumes distichous, membranous, lower glumes caducous, lowest glume 2.5 mm long, upper glumes 5–6 mm long, 1.8–2.6 mm wide, hispidulous when young, glabrescent, lanceolate, cuspidate, keeled; rachilla elongated and incurved to sinuous between the two flowers, in fruiting spikelets flattened, 3-ribbed. *Perianth segments* present, bristles (6–)7–8, flattened, long plumose, 5–6 mm long, *c.* 3 times as long as the nutlet. *Stamens* 3; anther connective 4–6 mm long, white, drying dark purple, subulate; anthers *c.* 3 mm long, linear-oblong, base auriculate, with a scabrous apical appendage up to 0.8 mm long. *Style* 3-fid, base 5–6 mm long, glabrous, thin throughout, branches 5–7 mm long, hispidulous. *Nutlet* sessile, subovoid, subterete but somewhat trigonous, with 3 longitudinal ribs, maturing dark brown, apex brown, smooth, 1.5–1.7 mm long including the style base, *c.* 1 mm diam., mesocarp smooth, epidermal cells square–hexagonal, but inconspicuous; style base only slightly thickened, persistent, hispidulous, *c.* 0.3 mm long; embryo not examined. Photosynthetic pathway not examined.

Diagnostic characters: Distinctive in having culms with 5–10 nodes below the inflorescence; caudex present; inflorescence 10–35 cm wide, branches arcuate; rachilla curved around nutlet; and perianth segments (6)7 or 8, 5–6 mm long.

Distribution: A single species endemic to the Seychelles.

Etymology: From *xyron* (razor), referring to the razor sharp leaf lamina edges and the vernacular name (*Lerb razwar*) (Larridon *et al.* 2018a).

Xyroschoenus hornei (C.B.Clarke) Larridon, *Mol. Phyl. Evol.* 127: 207 (2018).

Basionym: *Schoenus hornei* C.B.Clarke in T.A.Durand & H.Schinz, *Consp. Fl. Afric.* 5: 657 (1894), *nom. cons. prop.; Lophoschoenus hornei* (C.B.Clarke) Stapf in Gibbs, *J. Linn. Soc. Bot.* 42: 181 (1914), *p.p.*, excl. *Wright.*;

Costularia hornei (C.B.Clarke) Kük., *Repert. Spec. Nov. Regni Veg.* 44: 189 (1938); *Tetraria hornei* (C.B.Clarke) T.Koyama, *J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot.* 8: 75 (1961).

Type: Seychelles: on mountains, Mahé Island, 1874, *J. Horne 626* (lecto: K 000244890*), *typ. cons. prop.* by Larridon *et al. Taxon* 65(5): 1225 (2017), recommended in Applequist, *Taxon* 69(2): 393 (2020); (isolecto: K 000244891*).

Costularia hornei var. *rectirhachilloidea* Kük., *Repert. Spec. Nov. Regni Veg.* 46: 28 (1939).

Type: Seychelles: Mahé Island, Cascade Estate, Feb. 1903, *Thomasset 171* (lecto designated by Henriette *et al. Phytotaxa* 231(1): 33 (2015): K).

Residual syntype: Seychelles: Praslin Island, Mar. 1899, *W. Schimper 136* (syn: B, *n.v.*).

[*Asterochaete elongata auct. non* Kunth: Baker, *Fl. Mauritius* 417 (1877).]

[*Schoenus xipholepis* (Baker) Summerh., *Bull. Misc. Inform. Kew* 1928: 394 (1928:). *p.p.* as to *Horne 626* only.]

Illustrations: Line drawing on sheet of *Horne 626* (K 000244890); Clarke (1909, t. 79, figs 5–7); Wise (1998, pl. 55); Porembski and Barthlott (2000, fig. 8.3); Larridon *et al.* (2018, fig. 1c); www.seychellesplantgallery.com/Native.html.

Description: As for the genus. (Figure 31).

Diagnostic characters: As for the genus.

Distribution: Endemic to the Seychelles where it is known from Curieuse, Félicité, Mahé (Bernica, Congo Rouge, Copolia, Glacis Sarcellas, Pérard, Sixpenny Hill, Trois Frères), Praslin (Midlands, Vallée de Mai) and Silhouette (Dans Giroffe, Mont Pot à Eau, Morne Blanc) Islands.

Habitat: Grows on the open fringes of granite outcrops where it can be dominant, in tropical dry forests and tropical moist lowland forests, and in areas of disturbance, in shallow sands and deep, heavy clay soils, from full sun to deep shade, from near sea level to mountain summits (see Wise 1998 for more details). Recorded in association with *Aphloia theiformis*, *Begonia sechellensis*, *Canthium bibracteatum*, *Costularia xipholepis*, *Curculigo seychellensis*, *Cyathea sechellarum*, *Cymbopogon citratus*, *Cynanchum viminale*, *Deckenia nobilis*, *Dianella ensifolia*, *Dicranopteris linearis*, *Dillenia ferruginea*, *Diospyros seychellarum*, *Dracaena angustifolia*, *Erythroxylum sechellarum*, *Euphorbia pyrifolia*, *Garnottia sechellensis*, *Gastonia crassa*, *Glionnetia sericea*, *Hypoxidia rhizophylla*, *Ixora pudica*, *Lycopodiella cernuua*, *Lodoicea maldivica*, *Malaxis seychellarum*, *Mapania floribunda*, *Medusagyne oppositifolia*, *Memecylon eleagni*, *Mimusops sechellarum*, *Nepenthes pervillei*, *Northea seychellana*, *Pandanus multispicatus*, *Pandanus sechellarum*, *Procris insularis*, *Protarum sechellarum*, *Seychellaria thomasetti*, *Soulamea terminalioides*, *Syzygium wrightii*, *Vanilla phalaenopsis* and *Verschaffeltia splendida*.

Phenology: Flowers recorded for January–May. Fruit recorded for August–September.

Specimens examined: SEYCHELLES: Praslin Island, [rec. 9 June 1892], *R. Alluaud s.n.* (P*); Mahé Island, Glacis Soncelles, Aug. 1982, *F. Friedman 3365* (P*); Mahé Island, Mont Blanc, May 1987, *F. Friedman 5112* (P*); Praslin Island, Midlands, Aug. 1985, *F. Friedman 5366* (P*); Praslin Island, Vallée de Mai, 24 June 1974, *G. Gusset & B. Jeune 219* (P*); Curieuse Island, 27 June 1974, *G. Gusset & B. Jeune 290* (P*); Mahé Island, 100 m alt., *J. Proctor 4468* (K, P*, WAG*); Mahé Island, Bernica Hill, 20 Jan. 1978, *S.A. Robertson 2521* (P*, WAG*); Mahé Island, Copolia, 14 Aug. 2014, *B. Senterre & E. Henriette 7107* (SEY*, P*, GENT, *n.v.*); Silhouette Island, Mont Pot à Eau, 18 Mar. 2008, *B. Senterre & J. Gerlach 5294* (SEY*, P*, GENT, *n.v.*); Silhouette Island, Mont Pot à Eau, 24 Sept. 2014, *B. Senterre & C. Morel 7108* (SEY*, P*, GENT, *n.v.*).

Conservation: While the area of occupancy is small (50 km^2), as this species occurs on several islands, grows in a range of habitats, and no immediate threats are known, it is listed as IUCN: Least Concern (Gerlach 2011). It occurs in Morne Seychellois National Park.

Etymology: The epithet honours the collector of the type specimen, John Horne (1835–1905), former director of the Pamplemousses Botanical Garden, Mauritius.

Common names: Known locally as Herbe rasoir, Lerb razwar, or l'herbe rasoir (razor herb), due to the very sharp, scabrous leaf margins.

Notes: Until recently, this species has been confused with *Costularia xipholepis*, which is not closely related. Henriette *et al.* (2015) clarified the taxonomy and historical confusion of names. As first noted by Summerhayes (1928) and discussed in detail by Larridon *et al.* (2017b), the name *Schoenus hornei* C.B.Clarke was not legitimately published since *Cladium xipholepis* Baker (1877) was included as a synonym. Larridon *et al.* (2017b) proposed conserving the name *Schoenus hornei* with a conserved type to maintain established usage. This has now been recommended (Applequist 2020) but has not yet been accepted.

Fig. 31. *Xyroschoenus hornei*, Seychelles, Mahé and Silhouette Islands. A. Habitat. B. Habit. C. Plant base. D. Leaf rosette. E. Cross-section of new leaves showing spirodistichous arrangement. F. Inflorescence. G. Inflorescence branchlets and flowering spikelets. H. Staminate spikelets. I. Elongate rachilla with fruit fallen. J. Elongate rachilla with slightly immature fruit. Photos A, E–J; by B. Senterre; B; by G. Gendron; C, D; by C. Morel; from www.seychellesplantgallery.com.

Readily distinguished from *Costularia xipholepis* (Baker) Henriette & Senterre, with which it can co-occur, by tristichous (*vs* distichous) leaves, with a well-defined midrib, elongate inflorescence with pendant branches (*vs* short with erect branches) and elongate, sinuous rachilla (*vs* short and straight).

Kükenthal (1939a: 28) gives a date of April 1875 for the collection of *G.* [sic] *Horne 626*, but this is more likely to be the date of receipt of the specimen examined, which may have been at B, but if so it has probably been destroyed.

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References

Archer C (2000) Cyperaceae. In: OA Leistner (Ed.) *Seed plants of southern Africa: families and genera*. pp. 594–605. (National Botanical Institute: Pretoria) http://biodiversityadvisor.sanbi.org/wp-content/themes/bst/keys/e-Key-20160604/Families/F_Cyperaceae.html

Archer C (2003) Cyperaceae. In: G Germishuizen and NL Meyer (Eds) *Plants of southern Africa: an annotated checklist*. *Strelitzia* 14: 1020–1047. (National Botanical Institute: Pretoria)

Baird AM (1977) Regeneration after fire in King's Park, Perth, Western Australia. *Journal of the Royal Society of Western Australia* 60: 1–22.

Baker JG (1877) *Flora Mauritius and the Seychelles—A description of the flowering plants and ferns of those islands*. (Reeve & Co.: London) http://gallica.bnf.fr/ark:/12148/bpt6k98113c

Barker RM (2005) James Drummond's plant collections today – a global dispersal. In SJJF Davies (Ed.) *The Drummond Symposium: a review of the work of James Drummond, the first Government Botanist in Western Australia. Held at Toodyay, Western Australia, by the Toodyay Naturalists' Club, August 27 2004. Curtin University of Technology. Department of Environmental Biology Bulletin no. 27*. pp. 40–57. (Curtin University of Technology. Department of Environmental Biology: Perth)

Barrett RL (2012) *Systematic studies in Cyperaceae tribe Schoeneae:* Lepidosperma *and allied genera*. PhD thesis, The University of Western Australia.

Barrett RL, Bruhl JJ, Goetghebeur P, Larridon I, Mills KR, Muasya AM, Plunkett GT, Wilson KL (2017) Tribe Schoeneae (Cyperaceae): the taxonomic iceberg of sedges. Pp. 126–126 in *XIX International Botanical Congress: abstract book I: oral presentations*. Shenzhen, China)

Barrett RL, Bruhl JJ, Wilson KL (2021a) *Netrostylis*, a new genus of Australasian Cyperaceae removed from *Tetraria*. *Telopea* 24: 53–60. https://dx.doi.org/10.7751/telopea14922

Barrett RL, Pin Tay E (2016) *Perth plants. A field guide to the bushland and coastal flora of Kings Park and Bold Park, Perth*. Second edn. (CSIRO Publishing: Melbourne)

Barrett RL, Taputuarai R, Meyer J-Y, Bruhl JJ, Wilson KL (2021b) Reassessment of the taxonomic status of the endemic Cyperaceae on Rapa Iti, Austral Islands, French Polynesia, with a new combination, *Morelotia involuta*. *Telopea* 24: 171–187. https://dx.doi.org/10.7751/telopea14922

Barrett RL, Wilson KL (2012) A review of the genus *Lepidosperma* (Cyperaceae: Schoeneae). *Australian Systematic Botany* 25: 225–294. https://doi.org/10.1071/SB11037

Barrett RL, Wilson KL, Bruhl JJ (2019) *Anthelepis*, a new genus for four mainly tropical species of Cyperaceae from Australia, New Caledonia and South East Asia. *Australian Systematic Botany* 32: 269–289. https://doi.org/10.1071/SB18047

Barrett RL, Wilson KL, Bruhl JJ (2020) Reinstatement and revision of the genus *Chaetospora* (Cyperaceae: Schoeneae). *Telopea* 23: 95–112. https://dx.doi.org/10.7751/telopea14345

Benl G (1937) Eigenartige Verbreitungseinrichtungen bei der Cyperaceen-gattung *Gahnia*, Forst. *Flora* 131: 369–386.

Benl G (1940a) Die Systematik der Gattung *Gahnia* Forst. *Botanisches Archiv* 40: 151–257.

Benl G (1940b) Nomina nova vel emendata generis *Gahniae* Forst. *Feddes Repertorium* 49: 30–34.

Benl G (1942) *Gahniocarpus*, eine neue Cyperacee aus der rheinischen Tertiärflora. *Zentralblatt für Mineralogie, Geologie und Paläontologie: Abt. B* 1942: 187–190.

Benl G (1950) Zur Systematik der Cyperaceengattung *Gahnia* Forst. *Botanische Jahrbucher* 75: 82–89.

Craig GF, Bennett M, Chambers W, Penglase EM, Taylor H, Tink E (2011) *Native plants of the Ravensthorpe region*. Second edn. (Ravensthorpe Wildflower Show Inc.: Ravensthorpe, W.A.)

Bentham G (1878) *Flora Australiensis: A description of the plants of the Australian Territory. Vol. VII. Roxburghiaceae to Filices*. (Lovell Reeve: London) https://doi.org/10.5962/bhl.title.141

Black JM (1934) Additions to the flora of South Australia No. 32. *Transactions of the Royal Society of South Australia* 58: 168–186. https://www.biodiversitylibrary.org/item/129835#page/192/mode/1up

Black JM (1943) *Flora of South Australia Part 1*. 2nd edn. (Government Printer: Adelaide)

Blake ST (1949) Notes on Australian Cyperaceae, VII. *The Proceedings of the Royal Society of Queensland* 60: 45–53.

Blake ST (1969) Studies in Cyperaceae. *Contributions of the Queensland Herbarium* 8: 1–48.

Boeckeler O (1874) Die Cyperaceen des Königlichen Herbarium zu Berlin. Die Rhynchosporeen. *Linnaea* 38: 223–544. https://www.biodiversitylibrary.org/item/10883#page/225/mode/1up

Bond P, Goldblatt P (1984) Plants of the Cape Flora: a descriptive catalogue. *Journal of South African Botany Supplement* 13: 1–455.

Brown AP, Thomson-Dans C, Marchant NG (1998) *Western Australia's Threatened Flora*. (Department of Conservation and Land Management: Perth, WA)

Brown FBH (1931) *Flora of Southeastern Polynesia. I, Monocotyledons. Bernice P. Bishop Museum Bulletin 84*. (The Museum: Honolulu, Hawaii)

Brown R (1810) *Prodromus florae Novae-Hollandiae et insulae van-Diemen*. (Taylor: London) https://www.biodiversitylibrary.org/item/21871#page/100/mode/1up

Browning JBM, Goetghebeur P (2017) *Sedge (Cyperaceae) genera of Africa and Madagascar*. (Troubador: Leicester, UK)

Browning JBM, Gordon-Gray KD (1995a) Studies in Cyperaceae in southern Africa. 26: Glume epidermal silica deposits as a character in generic delimitation of *Costularia* and *Cyathocoma* as distinct from *Tetraria* and other allies. *South African Journal of Botany* 61: 66–71.

Browning JBM, Gordon-Gray KD (1995b) Studies in Cyperaceae in southern Africa. 27: a contribution to knowledge of spikelet morphology in *Epischoenus* and the relationship of this genus to *Schoenus*. *South African Journal of Botany* 61: 147–152.

Bruhl JJ (1990) *Taxonomic relationships and photosynthetic pathways in the Cyperaceae*. PhD Thesis. (Australian National University, Canberra)

Bruhl JJ (1995) Sedge genera of the world: relationships and a new classification of the Cyperaceae. *Australian Systematic Botany* 8: 125–305. https://doi.org/10.1071/SB9950125

Bruhl JJ, Barrett RL, Barrett MD, Hodgon J, Verboom AG, Muasya AM, Henning JL, Simpson DA, Wilson KL, Morden C, Csiba L, Forest F, Chase MW (2008a) Testing monophyly within Schoeneae-a storehouse of phylogenetic diversity in Cyperaceae. p. 100 in *Monocots IV, Abstracts*. (Natural History Museum of Denmark: Copenhagen)

Bruhl JJ, Barrett RL, Barrett MD, Hodgon J, Csiba L, Verboom GA, Muasya AM, Henning JL, Simpson DA, Wilson KL, Morden C, Forest F, Chase MW (2008b) Phylogenetic relationships of Schoeneae (Cyperaceae): the end of the beginning [Abstract]. In: *Australian Systematic Botany Society 2008 National Conference Adelaide. Systematics in a changing environment*. (The University of Adelaide: Adelaide).

Bruhl JJ, Wilson KL (2008) Towards a comprehensive survey of C_3 and C_4 photosynthetic pathways in Cyperaceae. Pp. 99–148 in JT Columbus, EA Friar, JM Porter, LM Prince and MG Simpson (Eds) *Monocots: comparative biology and evolution–Poales. Aliso 23*. (Rancho Santa Ana Botanic Garden: Claremont, California) https://doi.org/10.5642/aliso.20072301.11

Bureš P, Muasya AM, Lipnerová I, Zedek F, Bauters K, Šmarda P, Viljoen J-A, Gonzalez Elizondo MS, Barrett RL, Goetghebeur P, Bruhl JJ, Mwachala G, Prychid CJ, Hroudová Z, Thomas WW, Wilson KL (2013) The evolution of genome size and base composition in Cyperid clade. In *Monocots V: 5th International Conference on Comparative Biology of Monocotyledons*. (New York Botanic Garden: New York)

Clarke CB (1894) Cyperaceae. In TA Durand and H Schinz (Eds) *Conspectus florae Africae*. Volume 5. pp. 526–692 (Jardin Botanique de l'Etat: Bruxelles)

Clarke CB (1897–1898) Cyperaceae. In WT Thiselton-Dyer (Ed.) *Flora Capensis: being a systematic description of the plants of the Cape Colony, Caffraria, & Port Natal (and neighbouring territories). Volume VII. Pontederiaceae to Gramineae. Parts I & II. Series VII*. 2nd edn. pp. 149–310. (Lovell Reeve & Co.: London)

Clarke CB (1904) Cyperaceae. In: Diels FLE, Pritzel EG. Fragmenta Phytographiae Australiae occidentalis. Beitrage zur Kenntnis der Pflanzen Westaustraliens, ihrer Verbreitung und ihrer Lebensverhaltnisse. *Botanische Jahrbücher fur Systematik, Pflanzengeschichte und Pflanzengeographie* 35: 77–83.

Clarke CB (1908) New genera and species of Cyperaceae. *Kew Bulletin Additional Series* 8: 1–196. https://www.biodiversitylibrary.org/page/33600037#page/5/mode/1up

Clarke CB (1909) *Illustrations of Cyperaceae. Prepared under the direction of the late Charles Baron Clarke*. (Williams & Norgate: London) https://doi.org/10.5962/bhl.title.25276

Compton RH (1976) Cyperaceae. In: The Flora of Swaziland. *Journal of South African Botany Supplementary Volume* 11: 58–72.

Costa SM, Vitta FA, Thomas WW, Muasya AM, Morokawa R, Bittrich V, Shepherd GJ, Do Carmo E Do Amaral, M (2021) An updated generic circumscription for Cryptangieae (Cyperaceae, Poales) based on a molecular phylogeny and a morphological character reconstruction. *Phytotaxa* 483: 211–228. https://doi.org/10.11646/phytotaxa.483.3.2

Crisp MD (1983) Plantae Preissianae Types at Lund. *Australian Systematic Botany Society Newsletter* 36: 4–6.

Däniker AU (1932) Ergebnisse der Reise von Dr. A. U. Däniker nach Neu-Kaledonien und den Loyalty-Inseln (1924/26). 4. Katalog der Pteridophyta und Embryophyta siphonogama. 1. Teil. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich* 77: 1–114.

D'Antonio CM, Hughes RF, Tunison JT (2011) Long-term impacts of invasive grasses and subsequent fire in seasonally dry Hawaiian woodlands. *Ecological Applications* 21: 1617–1628. https://doi.org/10.1890/10-0638.1

Davidge C (1978) Ecology of baboons (*Papio ursinus*) at Cape Point. *Zoologica Africana* 13: 329–350. https://doi.org/10.1080/00445096.1978.11447633

Diels FLE, Pritzel EG (1904) Fragmenta Phytographiae Australiae occidentalis. Beitrage zur Kenntnis der Pflanzen Westaustraliens, ihrer Verbreitung und ihrer Lebensverhaltnisse. *Botanische Jahrbücher fur Systematik, Pflanzengeschichte und Pflanzengeographie* 35: 56–662.

de Lange PJ, Murray BG, Datson PM (2004) Contributions to a chromosome atlas of the New Zealand flora – 38. Counts for 50 families. *New Zealand Journal of Botany* 42: 873–904. https://doi.org/10.1080/002885X.2004.9512936

de Lange PJ, Rolfe JR, Barkla JW, Courtney SP, Champion PD, Perrie LR, Beadel SM, Ford KA, Breitwieser I, Schönberger I, Hindmarsh-Walls R, Heenan PB, Ladley, K (2018) *Conservation status of New Zealand indigenous vascular plants, 2017*. New Zealand Threat Classification Series 22. (Department of Conservation, Wellington, New Zealand)

Dell B, Bennett IJ (1986) *The flora of Murdoch University: a guide to the native plants on campus*. (Murdoch University Murdoch, Western Australia)

Demenois J, Rey F, Stokes A, Carriconde F (2017) Does arbuscular and ectomycorrhizal fungal inoculation improve soil aggregate stability? A case study on three tropical species growing in ultramafic Ferralsols. *Pedobiologia* 64: 8–14. https://doi.org/10.1016/j.pedobi.2017.08.003

Department of the Environment (2020). *Tetraria australiensis* in Species Profile and Threats Database, Department of the Environment, Canberra. Available from: http://www.environment.gov.au/sprat. [Accessed 25 Mar 2020]

Durand T (1888) *Index generum Phanerogamorum usque ad finem anni 1887 promulgatorum in Benthami et Hookeri "Genera plantarum" fundatus: cum numero specierum synonymis et area geographica*. (Sumptibus auctoris: Bruxellis) https://www.biodiversitylibrary.org/page/21135412

Edgar E (1970) Cyperaceae. In LB Moore and E Edgar (Eds) *Flora of New Zealand. Vol. II. Indigenous Trachyophyta. Monocotyledones except Gramineae*. pp. 167–285. (A.R. Shearer, Government Printer: Wellington)

Elliott TL, Barrett RL, Muasya AM (2019) A taxonomic revision of *Schoenus cuspidatus* and allies (Cyperaceae, tribe Schoeneae) –– Part 1. *South African Journal of Botany* 121: 519–535. https://doi.org/10.1016/j.sajb.2018.11.021

Elliott TL, Muasya AM (2017) Taxonomic realignment in the southern African *Tetraria* (Cyperaceae, tribe Schoeneae; *Schoenus* clade). *South African Journal of Botany* 112: 354–360. http://dx.doi.org/10.1016/j.sajb.2017.06.011

Elliott TL, Muasya AM (2018) A taxonomic revision of *Schoenus compar* - *Schoenus pictus* and allies (Cyperaceae, tribe Schoeneae) with three new species described from South Africa. *South African Journal of Botany* 114: 303–315. https://doi.org/10.1016/j.sajb.2017.11.020

Elliott TL, Muasya AM (2019) Three new species and a new combination among Southern African *Schoenus* (Cyperaceae, tribe Schoeneae). *Phytotaxa* 401: 267–275. https://doi.org/10.11646/phytotaxa.401.4.4

Elliott TL, Muasya AM (2020) A taxonomic revision of the *Epischoenus* group of *Schoenus* (Cyperaceae, tribe Schoeneae). *South African Journal of Botany* 135: 296–316. https://doi.org/10.1016/j.sajb.2020.08.029

Elliott TL, van Mazijk R, Barrett RL, Bruhl JJ, Joly S, Muthaphuli N, Wilson KL, Muasya AM (2021) Assessing the biogeographic history and diversification patterns of the austral temperate genus *Schoenus* (Cyperaceae). *Journal of Systematics and Evolution* Online early. https://doi.org10.1111/jse.12742.

Erickson R (1969) *The Drummonds of Hawthornden*. (Lamb Paterson Pty Ltd: Perth)

Evans, R, Willers N, Mitchell D (2003) *Threatened flora of the Swan Region*. Unpublished report to the Department of Conservation and Land Management and Environment Australia.

Forbes PL (1987) Cyperaceae. In TK Lowrey and S Wright (Eds) *The Flora of the Witwatersrand Vol. 1: The Monocotyledonae*. pp. 49. (Witwatersrand University Press: Johannesburg)

Forbes VS (1986) *Carl Peter Thunberg: travels at the Cape of Good Hope, 1772–1775*. Van Riebeeck Society Second Series No. 17. (Van Riebeeck Society: Cape Town)

Forster G (1786) *Florulae insularum Australium: Prodromus*. (Gottingae: J.C. Dietrich) https://www.biodiversitylibrary.org/page/11162995#page/97/mode/1up

Gaudichaud-Beaupré C (1827) Botanique. In: de Freycinet LCD (Ed.) *Voyage Autour du Monde ... sur les Corvettes de S.M. l'Uranie et la Physicienne. Part 4. Botanique, 1 vol. in-4.° et Atlas de 120 Planches in-folio. Des Planches*. (Ministère de la marine et des colonies: Paris) https://doi.org/10.5962/bhl.title.152367

Gaudichaud-Beaupré C (1829) Botanique. In: de Freycinet LCD (Ed.) *Voyage Autour du Monde ... sur les Corvettes de S.M. l'Uranie et la Physicienne. Part 4. Botanique, 1 vol. in-4.° et Atlas de 120 Planches in-folio. [Livre 10]* (Ministère de la marine et des colonies: Paris) https://www.biodiversitylibrary.org/item/98627#page/432/mode/1up

Gerlach J (2011) *Costularia hornei*. The IUCN Red List of Threatened Species 2011: e.T193434A8860056. https://dx.doi.org/10.2305/lUCN.UK.2011-2.RLTS.T193434A8860056.en. [Accessed 24 April 2020]

Gibbs AK, Wilson KL, Barrett RL, Muasya AM, Verboom GA, Musili PM, Bruhl JJ (2011) Dense sampling for assessment of monophyly in Schoeneae, a morphologically diverse tribe of Cyperaceae. In *International Botanical Congress 2011. Book of abstracts*. Melbourne. (Ed. KL Wilson) pp. 246–247. (IBC)

Goetghebeur P (1986) *Genera Cyperaceaerum. Een bijdrage tot de kennis van de morfologie, systematiek en fylogenese van de Cyperaceae-genera*. D.Sc. thesis, Rijksuniversiteit Gent [State University Gent].

Goetghebeur P (1998) Cyperaceae. Pp. 141–190 in K Kubitzki, H Huber, PJ Rudall, PS Stevens and T Stützel (Eds) *The families and genera of Vascular plants*. (Springer-Verlag: Berlin) https://doi.org/10.1007/978-3-662-03531-3_15

Gonin M, Gensous S, Lagrange A, Ducousso M, Amir H, Jourand P (2013) Rhizosphere bacteria of *Costularia* spp. from ultramafic soils in New Caledonia: diversity, tolerance to extreme edaphic conditions, and role in plant growth and mineral nutrition. *Canadian Journal of Microbiology* 59: 164–174. http://dx.doi.org/10.1139/cjm-2012-0570

Gordon-Gray KD (1995) Cyperaceae in Natal. *Strelitzia* 2: 1–218.

Govaerts R, Simpson DA, Bruhl JJ, Egorova T, Goetghebeur P, Wilson KL (2007) *World Checklist of Cyperaceae: sedges*. (Kew Publishing: London)

Hammer TA, Davis RW, Thiele KR (2019) Of a different feather: two new species of featherheads from the *Ptilotus macrocephalus* (Amaranthaceae) complex. *Australian Systematic Botany* 32: 61–70. https://doi.org/10.1071/SB18065

Hanekom N, Southwood A, Ferguson M (1989) A vegetation survey of the Tsitsikamma Coastal National Park. *Koedoe* 32: 47–66.

Hansen B, Wagner P (1998) A Catalogue of the herbarium specimens from Captain Cook's first and second expeditions housed in the Copenhagen Herbarium (C). *Allertonia* 7(4): 307–357.

Heller AA (1896) XLVIII. Observation on the ferns and flowering plants of the Hawaiian Islands. *Minnesota Botanical Studies* 1: 760–922.

Henriette E, Larridon I, Morel C, Goetghebeur P, Senterre B (2015) Revision of the genus *Costularia* (Cyperaceae: Schoeneae) for the flora of the Seychelles, including the rediscovery and resurrection of a rare endemic species. *Phytotaxa* 231: 31–41. http://dx.doi.org/10.11646/phytotaxa.231.1.3

Hiepko P (1969) Von J. R. und G. Forster gesammelte Pflanzen im Herbar Willdenow in Berlin [Plants collected by J. R. and G. Forster in the Willdenow Herbarium at Berlin (B)]. *Willdenowia* 5: 279–294.

Hooker WJ, Hooker JD (1883) *Icones Plantarum Vol. 15*. (Reeve & Co.: London)

Imada CT (Ed.) (2012) *Hawaiian native and naturalized vascular plants checklist (December 2012 update). Bishop Museum Technical Report 60*. (Hawaii Biological Survey, Bishop Museum: Honolulu, Hawai'i)

Jessop JP, Weber JZ (1986) Cyperaceae. In JP Jessop, HR Toelken (Eds) *Flora of South Australia* (edn 4). Vol. 4. pp. 2001–2053. (South Australian Government Printing Division: Adelaide)

Kaphahn S (1905) Beiträge zur anatomie der Rhynchosporeenblätter und zur Kenntnis der Verkieselungen. *Beihefte zum botanischen Centralblatt. Erste Abteilung, Anatomie, Histologie, Morphologie und Physiologie der Pflanzen* 18: 233–272. https://www.biodiversitylibrary.org/item/27439#page/269/mode/1up

Keeble J (2017) *Field guide to Hi Vallee Farm. A revised photographic guide to the kwongan bushland diversity on Don and Joy Williams' property Tootbardie Road, Badgingarra, Western Australia*. (Jolanda Keeble: Perth)

Keighery GJ (1993) Re-discovery of *Tetraria australiensis* C. B. Clarke (Cyperaceae). *The Western Australian Naturalist* 19: 268.

Kern JH (1958) Florae Malesianae precursores XVII. Notes on Malaysian and some S.E. Asian Cyperaceae V. *Blumea - Biodiversity, Evolution and Biogeography of Plants* 9: 215–236.

Kern JH (1962) On the delimitation of the genus *Gahnia* (Cyperaceae). *Acta Botanica Neerlandica* 11: 216–224.

Kern JH (1974) Cyperaceae. In CGGJ van Steenis (Ed.) *Flora Malesiana Series I*. pp. 435–753 (Wolters-Noordhoff Publishing: Groningen)

Koyama TM (1990) Cyperaceae. In WL Wagner, DR Herbst and SH Sohmer (Eds) *Manual of the flowering plants of Hawai'i. Volume 2*. pp. 1381–1436. (University of Hawai'i Press and Bishop Museum Press: Honolulu)

Koyama TM (1999) Cyperaceae. In WL Wagner, DR Herbst and SH Sohmer (Eds) *Manual of the flowering plants of Hawai'i. Volume 2. Bishop Museum Special Publication 97*. Revised edn. pp. 1381–1436. (University of Hawai'i Press and Bishop Museum Press: Honolulu)

Kükenthal G (1931) Cyperaceae novae vel minus cognitae. X. *Repertorium Specierum Novarum Regni Vegetabilis* 29: 187–202. https://doi.org/10.1002/fedr.19310291106

Kükenthal G (1938) Vorarbeiten zu einer monographie der Rhynchosporoideae. II. *Repertorium Specierum Novarum Regni Vegetabilis* 44: 65–101. https://doi.org/10.1002/fedr.19380440502

Kükenthal G (1939a) Vorarbeiten zu einer Monographie der Rhynchosporoideae. IV. *Repertorium Specierum Novarum Regni Vegetabilis* 46: 13–32.

Kükenthal G. (1939b) Vorarbeiten zu einer Monographie der Rhynchosporoideae. V. *Repertorium Specierum Novarum Regni Vegetabilis* 46: 65–76.

Kükenthal G (1940) Vorarbeiten zu einer Monographie der Rhynchosporoideae. IX. *Repertorium Novarum Specierum Regni Vegetabilis* 48: 195–250. https://doi.org/10.1002/fedr.4870481205

Kükenthal G (1943) Vorarbeiten zu einer monographie der Rhynchosporoideae. XIII. *Repertorium Specierum Novarum Regni Vegetabilis* 52: 52–111. https://doi.org/10.1002/fedr.19430520105

Kükenthal G (1944) Vorarbeiten zu einer monographie der Rhynchosporoideae. XV. *Repertorium Novarum Specierum Regni Vegetabilis* 53: 187–219. https://doi.org/10.1002/fedr.19440530304

Kunth CS (1837) *Enumeratio plantarum omnium hucusque cognitarum, secundum familias naturales disposita, adjectis characteribus, differentiis et synonymis, auctore Carolo Sigismundo Kunth*. (J. G. Cottae: Stutgardiae)

Lagrange A, Ducousso M, Jourand P, Majorel C, Amir H (2011) New insights into the mycorrhizal status of Cyperaceae from ultramafic soils in New Caledonia. *Canadian Journal of Microbiology* 57: 21–28.

Lander NS (1987) Asteraceae specimens collected by Johann August Ludwig Preiss. *Kingia* 1: 9–19.

Larridon I, Bauters K, Semmouri I, Viljoen J-A, Prychid CJ, Muasya AM, Bruhl JJ, Wilson KL, Senterre B, Goetghebeur PA (2018a) Molecular phylogenetics of the genus *Costularia* (Schoeneae, Cyperaceae) reveals multiple distinct evolutionary lineages. *Molecular Phylogenetics and Evolution* 126: 196–209. https://doi.org/10.1016/j.ympev.2018.04.016

Larridon I, Govaerts R, Goetghebeur P (2017b) (2554) Proposal to conserve the name *Schoenus hornei* (Cyperaceae) with a conserved type. *Taxon* 66: 1225–1226.

Larridon I, Rabarivola L, Xanthos M, Muasya AM (2019) Revision of the Afro-Madagascan genus *Costularia* (Schoeneae, Cyperaceae): infrageneric relationships and species delimitation. *PeerJ* 7: e6528. https://doi.org/10.7717/peerj.6528

Larridon I, Verboom GA, Muasya AM (2017a) (2555) Proposal to conserve the name *Tetraria* (Cyperaceae) with a conserved type. *Taxon* 66: 1226–1227. https://doi.org/10.12705/665.22

Larridon I, Verboom GA, Muasya AM (2018b) Revised delimitation of the genus *Tetraria*, nom. cons. prop. (Cyperaceae, tribe Schoeneae, *Tricostularia* clade). *South African Journal of Botany* 118: 18–22. https://doi.org/10.1016/j.sajb.2018.06.007

Larridon I, Villaverde T, Zuntini AR, Pokorny L, Brewer GE, Epitawalage N, Fairlie I, Hahn M, Kim JT, Maguilla E, Maurin O, Xanthos M, Hipp AL, Forest F, Baker WJ (2020a) Tackling rapid radiations with targeted sequencing. *Frontiers in Plant Science* 10: 1655. https://doi.org/10.3389/fpls.2019.01655

Larridon I, Zuntini AR, Barrett RL, Wilson KL, Bruhl JJ, Goetghebeur P, Baker WJ, Brewer GE, Epitawalage N, Fairlie I, Forest F, Kikuchi I, Pokorny L, Spalink D, Simpson DA, Muasya AM, Roalson EH (2021a) Resolving the generic limits in Cyperaceae tribe Abildgaardieae using targeted sequencing. *Botanical Journal of the Linnean Society* Online early https://doi.org/10.1093/botlinnean/boaa099

Larridon I, Zuntini AR, Léveillé-Bourret É, Barrett RL, Starr JR, Muasya AM, Villaverde T, Bauters K, Brewer GE, Bruhl JJ, Costa SM, Elliott TL, Epitawalage N, Escudero M, Fairlie I, Goetghebeur P, Hipp AL, Jiménez-Mejías P, Sabino Kikuchi IAB, Luceño M, Márquez-Corro JI, Martín-Bravo S, Maurin O, Pokorny L, Roalson EH, Semmouri I, Simpson DA, Spalink D, Thomas WW, Wilson KL, Xanthos M, Forest F, Baker WJ (2021b) A new classification of Cyperaceae (Poales) supported by phylogenomic data. *Journal of Systematics and Evolution* JSE-2020-09-229: In press.

Lehmann JGC (1844) *Novarum et minus cognitarum stirpium pugillus VIII, addita enumeratione plantarum omnium in his pugillis descriptarum*. (Hamburgi, J.A. Meissneri) https://www.biodiversitylibrary.org/item/97774#page/430/mode/1up

Lepschi BJ (2012) *The taller tree of liff*. (Over Educated Publications: Canberra)

Lestiboudois TG (1819) *Essai sur la famille de Cypéracées*. (Didot jeune: Paris)

Levyns MR (1947) *Tetraria* and related genera, with special reference to the flora of the Cape Peninsula. *Journal of South African Botany* 13: 73–93.

Levyns MR (1950) Cyperaceae. In: RS Adamson and TM Salter (Eds) *Flora of the Cape Peninsula*. pp. 97–132. (Juta & Co.: Cape Town)

Levyns MR (1959) A revision of *Epischoenus* C.B. Cl. *Journal of South African Botany* 25: 69–82.

Liang S, Bruhl JJ, Wilson KL (2010) *Tricostularia*. Pp. 260–260 in Wu Zhengyi, PH Raven and Hong Deyuan (Eds) *Flora of China, Volume 23: Acoraceae–Cyperaceae*. (Missouri Botanical Garden Press: Missouri)

Marchant NG (1990) The Western Australian collecting localities of J. A. L. Preiss. Pp. 131–135 in PS Short (Ed.) *History of systematic botany in Australasia*. (Australian Systematic Botany Society: Victoria)

Marloth R (1915) *The flora of South Africa: with synopical tables of the genera of the higher plants. Volume 4: Monocotyledones*. (Darter Bros. & Company: Cape Town)

McGillivray DJ (1975) Johann August Ludwig Preiss (1811–1883) in Western Australia. *Telopea* 1: 1–18.

Metcalfe CR (1971) *Anatomy of the monocotyledons. V. Cyperaceae*. (Clarendon Press: Oxford)

Meyer J-Y (2004) Threat of invasive alien plants to native flora and forest vegetation of Eastern Polynesia. *Pacific Science* 58: 357–375.

Meyer J-Y, Laitame T, Gaertner J-C (2019) Short term recovery of native vegetation and threatened species after restoration of a remnant forest in a small oceanic island of the South Pacific. *Plant Ecology and Diversity* 12: 75–85. https://doi.org/10.1080/17550874.2019.1584651

Meyer J-Y, Chevillote, H, Motley TJ (2015) Vascular flora, general traits and main threats. In: Meyer J-Y, Claridge EM (Eds) *Terrestrial biodiversity of the Austral Islands, French Polynesia*. Patrimonines Naturels (Book 72) pp. 117–132. (Muséum National d'Histoire Naturelle: Paris)

Moar NT, Wilmshurst JM (2003) A key to the pollen of New Zealand Cyperaceae. *New Zealand Journal of Botany* 41: 325–334.

Morris DI (1994) *Tricostularia*. Pp. 127–128 in WM Curtis and DI Morris (Eds) *The student's flora of Tasmania. Part 4B Angiospermae: Alismataceae to Burmanniaceae*. 2nd edn. (St David's Park Publishing: Hobart, Tasmania)

Muasya AM (2016) The changing generic concepts in Cyperaceae — Cosmopolitan mega-genera and polyphyly of southern African taxa. *South African Journal of Botany* 103: 337. https://doi.org/10.1016/j.sajb.2016.02.125

Muasya AM, Bruhl JJ, Simpson DA, Culham A, Chase MW (2000) Suprageneric phylogeny of Cyperaceae: a combined analysis. Pp. 593–601 in KL Wilson and DA Morrison (Eds) *Monocots. Systematics and evolution*. (CSIRO Publishing: Collingwood)

Muasya AM, Simpson DA, Verboom GA, Goetghebeur P, Naczi RFC, Chase MW, Smets EF (2009) Phylogeny of Cyperaceae based on DNA sequence data: current progress and future prospects. *The Botanical Review* 75: 2–21. https://doi.org/10.1007/s12229-008-9019-3

Mueller FJH von (1875) *Fragmenta Phytographiae Australiae. Vol. 9*. (Melbourne Printers: Melbourne) https://www.biodiversitylibrary.org/item/7226#page/1/mode/1up

Musili PM, Gibbs AK, Wilson KL, Bruhl JJ (2016) *Schoenus* (Cyperaceae) is not monophyletic based on ITS nrDNA sequence data. *Australian Systematic Botany* 29: 265–283. https://doi.org/10.1071/SB15046

Nees von Esenbeck CGD (1832) Cyperaceae Capenses Ecklonianae. *Linnaea* 7: 491–537. https://www.biodiversitylibrary.org/page/35308617

Nees von Esenbeck CGD (1834) New genera of Cyperaceae. In: GA Walker-Arnott, New genera of plants. *Edinburgh New Philosophical Journal* 17: 260–268. https://www.biodiversitylibrary.org/item/20108#page/274/mode/1up

Nees von Esenbeck CGD (1835) Übersicht der Cyperaceengattungen. *Linnaea* 9: 273–306. https://www.biodiversitylibrary.org/item/109555#page/279/mode/1up

Nees von Esenbeck CGD (1841) Characters of new genera and species of New Holland Cyperacece, Restiacece, and Juncacece. *The Annals and Magazine of Natural History* 6: 45–50. https://www.biodiversitylibrary.org/item/19590#page/63/mode/1up

Nees von Esenbeck CGD (1846) Cyperaceae. Pp. 72–94 in JGC Lehmann (Ed.) *Plantae Preissianae sive enumeratio plantarum, quas in Australasia Occidentali et Meridionali-occidentale annis 1838–1841 collegit Ludovicus Preiss, Ph. Dr.* (Meissner: Hamburg) https://www.biodiversitylibrary.org/item/9228#page/76/mode/1up

New Zealand Plant Conservation Network (2020) *Morelotia affinis*. http://nzpcn.org.nz/flora_details.aspx?ID=801 [Accessed 23 April 2020]

Nordenstam B (1980) The herbaria of Lehmann and Sonder in Stockholm, with special reference to the Ecklon and Zeyher collection. *Taxon* 29: 279–291.

Perrier N, Amir H, Colin F (2006) Occurrence of mycorrhizal symbioses in the metal-rich lateritic soils of the Koniambo Massif, New Caledonia. *Mycorrhiza* 16: 449–458. https://doi.org/10.1007/s00572-006-0057-6

Podlech D (1967) *Cyperaceae. Prodromus einer Flora von Südwestafrika 165*. (Lehre: Verlag. von J. Cramer)

Porembski S, Barthlott W (Eds) (2000) *Inselbergs. Biotic diversity of isolated rock outcrops in tropical and temperate regions*. Ecological Studies Vol. 146. (Springer, Berlin) https://doi.org/10.1007/978-3-642-59773-2

Posada D (2008) jModelTest: Phylogenetic Model Averaging. *Molecular Biology and Evolution* 25: 1253–1256. https://doi.org/10.1093/molbev/msn083

Prebble M, Anderson A (2012) The archaeobotany of Rapan rockshelter deposits. In *Taking the high ground: the archaeology of Rapa, a fortified island in remote East Polynesia*. A Anderson and DJ Kennett (Eds). pp. 77–95. (ANU E Press: Canberra)

Presl CB (1829) *Lepisia, novum plantarum genus*. [preprint] (C.Presl: Pragae)

Raynal J (1974) Notes Cypérologiques. 22. Les *Costularia* de Nouvelle-Calédonie. *Adansonia, sér. 2*, 14: 337–377.

Rebelo AG, Boucher C, Helme N, Mucina L, Rutherford MC (2006) Fynbos biome. *Strelitzia* 19: 53–219.

Richard A (1832) *Essai d'une Flore de la Nouvelle-Zelande*. (Tastu: Paris)

Robertson SA (1989) *Flowering plants of Seychelles (An annotated checklist of angiosperms and gymnosperms with line drawings)*. (Royal Botanic Gardens, Kew: Kew)

Rottbøll CF (1773) *Descriptionum et iconum rariores et pro maxima parte novas plantas illustrantium*. (Sumptibus Societatis Typographicae: Hafniae)

Rye BL (1987) Cyperaceae. Pp. 870–906 in NG Marchant and JR Wheeler (Eds) *Flora of the Perth Region*. (Western Australian Herbarium: Perth)

Sandiford EM, Barrett S (2010) *Albany Regional Vegetation Survey, extent type and status*. Unpublished report. (Department of Environment and Conservation: Perth, Western Australia)

Schönland S (1922) Introduction to South African Cyperaceae. *Memoirs of the Botanical Survey of South Africa* 3: 1–72.

Schrader HA (1821) Analecta ad floram Capensem. Sect. II. Cyperaceae. Gramineae. *Göttingische gelehrte Anzeigen* 3: 2065–2079.

Scott J, Negus P (2002) *Field guide to the wildflowers of Australia's south west: Augusta – Margaret River region*. (Cape to Cape Publishing: North Fremantle)

Semmouri I, Bauters K, Léveillé-Bourret É, Starr JR, Goetghebeur P, Larridon I (2019) Phylogeny and systematics of Cyperaceae, the evolution and importance of embryo morphology. *The Botanical Review* 85: 1–39. https://doi.org/10.1007/s12229-018-9202-0

Simpson DA, Muasya AM, Alves MV, Bruhl JJ, Dhooge S, Chase MW, Furness CA, Ghamkhar K, Goetghebeur P, Hodgkinson TR, Marchant AD, Reznicek AA, Nieuwborg R, Roalson EH, Smets EF, Starr JR, Thomas WW, Wilson KL, Zhang X (2008) Phylogeny of Cyperaceae based on DNA sequence data–a new *rbc*L analysis. Pp. 72–83 in JT Columbus, EA Friar, JM Porter, LM Prince and MG Simpson (Eds) *Monocots: comparative biology and evolution–Poales. Aliso 23*. (Rancho Santa Ana Botanic Garden: Claremont, California)

Slingsby JA, Britton MN, Verboom GA (2014) Ecology limits the diversity of the Cape flora: phylogenetics and diversification of the genus *Tetraria*. *Molecular Phylogenetics and Evolution* 72: 61–70.

Slingsby JA, Verboom GA (2006) Phylogenetic relatedness limits co-occurrence at fine spatial scales: evidence from the Schoenoid sedges (Cyperaceae: Schoeneae) of the Cape Floristic Region, South Africa. *The American Naturalist* 168: 14–27. https://doi.org/10.1086/505158

Smith SY, Collinson ME, Rudall PJ, Simpson DA (2010) Cretaceous and Paleogene fossil record of Poales: review and current research. Pp. 333–356 in O Seberg, G Petersen, AS Barfod and JI Davis (Eds) *Diversity, phylogeny, and evolution in the monocotyledons. Proceedings of the Fourth International Conference on the Comparative Biology of the Monocotyledons and the Fifth International Symposium on Grass Systematics and Evolution*. (Aarhus University Press: Århus)

St John H (1958) The status of "*Gahnia affinis*" and "*G. gahniaeformis*" (Cyperaceae) of Polynesia. Pacific plant studies 16. *Webbia* 13: 331–342. https://doi.org/10.1080/00837792.1958.10669679

St John H (1984) *Machaerina* and *Uncinia* (Cyperaceae) on Rapa, Austral Islands. – Pacific plant studies 41. *Nordic Journal of Botany* 4: 57–60. https://doi.org/10.1111/j.1756-1051.1984.tb01972.x

Staff IA, Clifford HT (1987) On arborescence in *Gahnia clarkei* and *Gahnia sieberiana*. *Annals of Botany* 60: 33–39. https://doi.org/10.1093/oxfordjournals.aob.a087419

Stafleu FA, Cowan RS (1976) *Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types. Volume 1. A–G*. Second edn. (Bohn, Scheltema & Holkema: Utrecht) https://www.biodiversitylibrary.org/page/33120144

Stapf O, Turrill WB (1914) Cyperaceae. In: Gibbs, L.S. (Ed.), A contribution to the flora and plant formations of Mount Kinabalu and the highlands of British North Borneo. *Journal of the Linnean Society, Botany* 42: 173–185.

Summerhayes VS (1928) New plants from the Seychelles. *Bulletin of Miscellaneous Information* (*Royal Gardens, Kew*) 1928: 388–395. http://dx.doi.org/10.2307/4107106

Takeda M, Ueno O, Samejima M, Ohtani T (1985) An investigation for the occurrence of C_4 photosynthesis in the Cyperaceae from Australia. *The Botanical Magazine, Tokyo* 98: 393–411. https://doi.org/10.1007/BF02488504

Thunberg CP (1794) *Prodromus plantarum Capensium: quas in promontorio Bonæ Spei Africes, annis 1772–1775*. (J. Edman: Upsaliæ) https://www.biodiversitylibrary.org/page/3553138#page/28/mode/1up

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AK, Prado J, Price MJ, Smith GF (2018) (Eds) *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159*. (Koeltz Botanical Books: Glashütten) https://doi.org/10.12705/Code.2018

Vanhecke L (1974) Embryography of some genera of the Cladiinae and the Gahniinae (Cyperaceae) with additional notes on their fruit anatomy. *Bulletin du Jardin Botanique National de Belgique* 44: 367–400. https://doi.org/10.2307/3667678

Vánky K, Shivas RG (2008) *Fungi of Australia. The smut fungi*. (Australian Biological Resources Study: Canberra and CSIRO Publishing: Melbourne)

Vánky K (2009) Taxonomic studies on Ustilaginomycetes – 29. *Mycotaxon* 110: 289–324.

Verboom GA (2006) A phylogeny of the schoenoid sedges (Cyperaceae: Schoeneae) based on plastid DNA sequences, with special reference to the genera found in Africa. *Molecular Phylogenetics and Evolution* 38: 79–89. https://doi.org/10.1016/j.ympev.2005.05.012

Viljoen J-A, Muasya AM, Barrett RL, Bruhl JJ, Gibbs AK, Slingsby JA, Wilson KL, Verboom AG (2013) Radiation and repeated transoceanic dispersal of Schoeneae (Cyperaceae) through the Southern Hemisphere. *American Journal of Botany* 100: 2494–2508. https://doi.org/10.3732/ajb.1300105

Villaverde T, Jiménez-Mejías P, Luceño M, Roalson EH, Hipp AL, and the Global Carex Group: Park J, Larridon I, Martín-Bravo S, Naczi RFC, Reznicek AA, Escudero M, Ford BA, Gebauer S, Hoffmann MH, Simpson DA, Starr JR, Wilson KL (2020) A new classification of *Carex* subgenera supported by a HybSeq backbone phylogeny. *Botanical Journal of the Linnean Society* 194: 141–163. https://doi.org/10.1093/botlinnean/boaa042

Wheeler JR, Graham L (2002) Cyperaceae. Pp. 263–298 in JR Wheeler (Ed.) *Flora of the South West. Bunbury, Augusta, Denmark. Flora of Australia Supplementary Series 12*. (Australian Biological Resources Study, Canberra, Conservation and Land Management, Como and University of Western Australia Press: Crawley)

White TJ, Bruns S, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In MA Innis, DH Gelfand, JJ Sninsky and TJ White (Eds) *PCR protocols: a guide to methods and applications*. pp. 315–322. (Academic Press: San Diego, California)

Wilkins CF, Sandiford EM (2020) *Gompholobium glabristylum* (Fabaceae), a new native pea from montane habitats in Stirling Range National Park. *Nuytsia* 31: 223–227. https://florabase.dpaw.wa.gov.au/science/nuytsia/977.pdf

Wilson KL (1980) Notes on some Australian species of Cyperaceae. *Telopea*. 1: 457–467. https://dx.doi.org/10.7751/telopea19803607

Wilson KL (1983) Plantae Preissianae specimens. *Australian Systematic Botany Society Newsletter* 34: 5–6.

Wilson KL (1993) Cyperaceae. Pp. 293–396 in GJ Harden (Ed.) *Flora of New South Wales*. (University of New South Wales Press: Kensington)

Wilson KL (1994a) New taxa and combinations in the family Cyperaceae in eastern Australia. *Telopea* 5: 589–625. https://dx.doi.org/10.7751/telopea19944989

Wilson KL (1994b) Cyperaceae. Pp. 238–356 in NG Walsh and TJ Entwisle (Ed.) *Flora of Victoria Volume 2. Ferns and allied plants, conifers and monocotyledons*. (Inkata Press: Melbourne)

Wilson KL, Bruhl JJ, Barrett RL, Gibbs AK, Musili PM, Plunkett GT (2012) Understanding the big genera of tribe Schoeneae (Cyperaceae). In: JA Wege, R Butcher, KA Shepherd and KL Lemson (Eds), *Australasian Systematic Botany Society Conference 2012 'Local knowledge, global delivery'*. Perth. p. 57. (ASBS, Perth)

Wise R (1998) *A fragile eden: portraits of the endemic flowering plants of the Granitic Seychelles*. (Princeton University Press: Princeton)

Wulff A, L'Huillier L, Véa C, Jaffré T (2010) Espèces indigènes utilisables en revégétalisation. In: L L'Huillier, T Jaffré and A Wulff (Eds) *Mines et Environnement en Nouvelle-Calédonie: les milieux sur substrats ultramafiques et leur restauration*. Pp. 231–344. (Éditions IAC: Nouméa, Nouvelle-Calédonie)

Zhang X, Marchant A, Wilson KL, Bruhl JJ (2004) Phylogenetic relationships of *Carpha* and its relatives (Schoeneae, Cyperaceae) inferred from chloroplast *trn*L intron and *trn*L—*trn*F integenic spacer sequences. *Molecular Phylogenetics and Evolution* 31: 647–657. https://doi.org/10.1016/j.ympev.2003.09.004

Zhang X, Bruhl JJ, Wilson KL, Marchant AD (2007) Phylogeny of *Carpha* and related genera (Schoeneae, Cyperaceae) inferred from morphological and molecular data. *Australian Systematic Botany* 20: 93–106. https://doi.org/10.1071/SB06023

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Appendix 1. Comparison of morphological features of genera and species in the *Tricostularia* clade. ? = attribute not known; C3 and C4 refer to photosynthetic pathway (see Bruhl & Wilson 2007).

Character	**Plant**											
Name	annual / perennial	tufted / open (rhizome elongate)	height (m)	rhizome thick / thin	rhizome diam. (mm)	pseudobulbous: Y/N/slightly	roots sand-binding: Y/N	clonal: Y/N	caudex: P/A	sheaths covering caudex: Y/N	sheath base fibrous: Y/N	sheath base colour
Ammothryon grandiflorum	perennial	tufted-open	0.7-1.5	thick	10-22	yes	yes	yes	present	yes	no	pale to reddish brown
Chaetospora	perennial	tufted	0.13-0.55	thin	0.8-3.4	yes	yes or no	yes	absent	yes	yes	reddish brown or straw coloured
Chaetospora curvifolia	perennial	tufted	0.13-0.5	thin	0.8-3.0	yes	yes	yes	absent	yes	yes	reddish brown
Chaetospora subbulbosa	perennial	tufted	0.15-0.55	thin	2-5	yes	no	yes	absent	yes	yes	reddish brown
Chaetospora turbinata	perennial	tufted	0.14-0.40	thin	1.2-3.4	yes	no	yes	absent	yes	yes	straw-coloured
Morelotia	perennial	tufted	0.2-1.2	thick	5-15	yes or no	yes or no	yes	absent	yes	yes or no	cream to pale to dark brown
Morelotia affinis	perennial	tufted	0.2-0.7	thick	5-10	slightly	no	yes	absent	yes	yes	cream to pale brown
Morelotia australiensis	perennial	tufted	0.3-1.3	thick	8-15	slightly	yes	yes	absent	yes	no	dark brown to blackish brown
Morelotia gahniiformis	perennial	tufted	0.2-0.7	thick	5-8	slightly	no	yes	absent	yes	yes	pale brown
Morelotia involuta	perennial	tufted	0.2-0.6	thick	10-15	no	no	yes	absent	yes	yes	pale to dark brown
Morelotia microcarpa	perennial	tufted	0.2-0.4(-0.6)	thick	6-8	yes	yes	yes	absent	yes	yes	pale brown
Morelotia octandra	perennial	tufted	0.7-1.2	thick	10-15	yes	yes	yes	absent	yes	yes	dark brown to blackish brown
Tetraria	perennial	tufted-open	0.3-3.0	thick or thin	1-45	no	yes	yes	absent or present	yes	yes (at least partial)	green to pale brown to dark brown
Tetraria arundinacea	perennial	tufted-open	1.5-3.0	thick	15-20	no	yes	yes	present	yes	yes	reddish brown to dark brown
Tetraria capillacea	perennial	tufted	0.3-0.6	thick	5-15	no	yes	yes	absent	yes	yes	chestnut-brown
Tetraria cernuua	perennial	tufted	0.3-0.7	thin	1-2	no	yes	yes	absent	yes	yes (margins only)	green to pale brown to dark brown
Tetraria thermalis	perennial	open-tufted	0.9-2.5	thick	20-45	slightly	yes	yes	present	yes	yes (at base only)	dark brown to blackish brown

(*Continued...*)

Character	**Plant**											
Name	annual / perennial	tufted / open (rhizome elongate)	height (m)	rhizome thick / thin	rhizome diam. (mm)	pseudobulbous: Y/N/slightly	roots sand-binding: Y/N	clonal: Y/N	caudex: P/A	sheaths covering caudex: Y/N	sheath base fibrous: Y/N	sheath base colour
Tricostularia	perennial	tufted	0.1-1.0(-1.3)	thin	0.7-2.1	no	yes	yes	absent	yes	yes or no	straw-coloured or pale to reddish brown
Tricostularia aphylla	perennial	tufted	0.3-0.6	thin	1.6-2.1	no	yes	yes	absent	yes	sometimes	pale brown
Tricostularia bennettiana	perennial	tufted	0.15-0.3	thin	1-1.5	no	yes	yes	absent	yes	no	pale brown
Tricostularia compressa	perennial	tufted	(0.15-)0.3-0.45	thin	0.7-1.2	no	yes	yes	absent	yes	no	pale brown
Tricostularia davisii	perennial	tufted	0.1-0.6	thin	8.8-1.2	no	yes	yes	absent	yes	no	pale brown
Tricostularia drummondii	perennial	tufted	0.5-0.8	thin	?	no	yes	yes	absent	yes	no	pale brown
Tricostularia exsul	perennial	tufted	0.4-1.0(-1.3)	thin	1.6-2.3	no	yes	yes	absent	yes	yes	pale brown
Tricostularia lepschii	perennial	tufted-open	0.15-0.4	thin	1-2.6	no	yes	yes	absent	yes	yes or no	pale brown
Tricostularia neesii	perennial	tufted	0.5-0.8	thin	0.9-1.6	no	yes	yes	absent	yes	no	pale to reddish brown
Tricostularia newbeyi	perennial	tufted	0.2-0.9	thin	1.5-2.5	no	yes	yes	absent	yes	no	pale brown
Tricostularia pauciflora	perennial	tufted	0.1-0.45(-70)	thin	1-2	no	yes	yes	absent	yes	no	pale to reddish brown
Tricostularia sandifordiana	perennial	open	0.3-0.9	thin	0.8-1.8	no	yes	yes	absent	yes	yes	straw-coloured or pale brown
Tricostularia sp. Albany	perennial	tufted	(0.4-)0.5-1	thin	?	no	yes	yes	absent	yes	?	?
Tricostularia sp. Mogumber	perennial	tufted	c. 0.4	thin	?	no	yes	yes	absent	yes	no	straw-coloured or pale brown
Tricostularia sp. Porongurup	perennial	tufted	c. 0.3	thin	?	no	yes	yes	absent	yes	?	?
Tricostularia sp. Two Peoples Bay	perennial	tufted	0.5-1	thin	?	no	yes	yes	absent	yes	no	pale to reddish brown
Xyroshoenus hornei	perennial	tufted	0.9-1.5(-2.0)	thick	20-50	no	no	yes	present	yes	sometimes	reddish to dark brown

(*Continued...*)

Character	**Culm**								
Name	slender / stout	erect / spreading	culms helicoid (spiralled)	no. nodes	culms angular / compressed (flattened) / terete to oval	culm diam. / width (mm)	culm height below inflorescence (cm)	culms ribbed / finely striate / smooth	culms glabrous / scabrous / other
Ammothryon grandiflorum	stout	erect	no	4-7	trigonous	2.5–7	55-80	finely striate	scabrous
Chaetospora	thin	erect	no	0	terete to compressed	0.6-2.5	11-53	finely striate, sometimes grooved	glabrous
Chaetospora curvifolia	thin	erect	no	0	terete to compressed	0.4-1.6	11-48	finely striate	glabrous
Chaetospora subbulbosa	thin	erect	no	0	terete to compressed	1.0-2.5	14-53	finely striate	glabrous
Chaetospora turbinata	thin	erect	no	0	terete to compressed	0.6-1.7	12-38	striate, sometimes grooved	glabrous
Morelotia	stout	erect	no	0, 1 or 3-4	trigonous or terete	1.0-5.5	6-100	striate to grooved	glabrous or rugulose
Morelotia affinis	stout	erect	no	0-2(-4)	trigonous	1.9-3.5	15-40	finely striate	glabrous
Morelotia australiensis	stout	erect	no	3-4	terete	2.0-5.5	15-100	striate	glabrous
Morelotia gahniiformis	stout	erect	no	1-3	trigonous	1.5-3.8	10-35	finely striate	glabrous
Morelotia involuta	stout	erect	no	1	trigonous	1.3-1.7	10-30	finely striate	glabrous
Morelotia microcarpa	stout	erect	no	1	trigonous	1.1-1.3	6-15(-25)	striate to grooved	rugulose-asperulous
Morelotia octandra	stout	erect	no	0 or 1	terete to trigonous at apex	1.0-3.5	55-85	striate	glabrous
Tetraria	stout or thin	erect to spreading	no	0-5	trigonous or terete	0.5-8	4-230	smooth or finely striate	glabrous
Tetraria arundinacea	stout	erect	no	3-4	trigonous	3-7	130-230	smooth but deeply grooved	glabrous
Tetraria capillacea	thin	erect	no	1-3	terete	1.5-3.1	30-60	finely striate	glabrous
Tetraria cernuua	thin	erect to spreading	no	0-1	terete	0.5-0.9	4-20	finely striate	glabrous
Tetraria thermalis	stout	erect	no	2-5	trigonous	4-8	50-120	smooth	glabrous

(*Continued...*)

Character	**Culm**								
Name	slender / stout	erect / spreading	culms helicoid (spiralled)	no. nodes	culms angular / compressed (flattened) / terete to oval	culm diam. / width (mm)	culm height below inflorescence (cm)	culms ribbed / finely striate / smooth	culms glabrous / scabrous / other
Tricostularia	stout or thin	erect to spreading	yes or no	0-5	compressed to terete	0.3-3.3	9-78	smooth or finely striate	glabrous
Tricostularia aphylla	stout	spreading (rarely erect)	yes	1-2(-3)	compressed	1.9-3.2	25-50	striate	glabrous
Tricostularia bennettiana	thin	erect	no	1(?-2)	terete	0.6-1.1	13-27	finely striate	glabrous
Tricostularia compressa	thin	erect	no	0	terete	0.4-0.6	28-42	smooth	glabrous
Tricostularia davisii	thin	erect	no	2	terete	0.3-0.8	9-58	finely striate	glabrous
Tricostularia drummondii	thin	erect	no	1-2	terete	0.7-1.0	45-75	finely striate	glabrous
Tricostularia exsul	thin	erect to spreading	no	2	terete	1.1-2.0	35-90(-120)	finely striate	glabrous
Tricostularia lepschii	thin	erect	no	0	terete	0.6-0.8	14-39	finely striate	glabrous
Tricostularia neesii	thin	erect	no	1-2	terete	0.5-1.5	48-78	finely striate	glabrous
Tricostularia newbeyi	thin	erect	no	1(-2)	terete	0.5-1.2	18-83	finely striate	glabrous
Tricostularia pauciflora	thin	erect to arcuate	no	0-2	terete	0.5-1.2	9-43(-68)	smooth	glabrous
Tricostularia sandifordiana	thin	erect	no	2-5	terete	0.7-1.7	26-87	finely striate	glabrous
Tricostularia sp. Albany	thin	erect	no	1(?+)	terete	0.6-1.2	(35-)45-100	finely striate	glabrous
Tricostularia sp. Mogumber	thin	erect to spreading	no	0	terete	?	c. 40	finely striate	glabrous
Tricostularia sp. Porongurup	thin	spreading	yes, slightly twisting	1(?+)	strongly compressed, almost flattened	1.2-1.9	c. 30	finely striate	glabrous
Tricostularia sp. Two Peoples Bay	thin	erect	no	1	terete	0.4-0.9	c. 50-95	finely striate	glabrous
Xyroshoenus hornei	stout	erect	no	5-10	trigonous	3-9	0.45-1.0(-1.4)	smooth	glabrous

(*Continued...*)

Character	**Leaves**			**Leaf sheath**						
Name	basal / cauline / both	bract- / leaf-like at base	spirotristichous / spirodistichous	body glabrous / scabrous / other	loose / clasping	length (mm)	broader than blade: Y/N	margin below blade hairy: Y/N	ligule: P/A	pseudopetiole: P/A
Ammothryon grandiflorum	both	leaf-like	spirotristichous	scabrous	loose	20–28(–38)	no	yes	absent	obscure or absent
Chaetospora	basal	leaf-like	spirodistichous	glabrous or scabrous	clasping	20-70	yes	yes	absent	obscure or absent
Chaetospora curvifolia	basal	leaf-like	spirodistichous	glabrous	clasping	20-40	yes	yes	absent	obscure or absent
Chaetospora subbulbosa	basal	leaf-like	spirodistichous	scabrous	clasping	20-40	yes	yes	absent	obscure or absent
Chaetospora turbinata	basal	leaf-like	spirodistichous	scabrous	clasping	40-70	yes	yes	absent	obscure or absent
Morelotia	both	leaf-like	spirodistichous	glabrous	loose or clasping	8-60	yes or equal	yes or no	absent	present, obscure or absent
Morelotia affinis	both	leaf-like	spirodistichous	glabrous	loose	35-60	yes	yes	absent	obscure or absent
Morelotia australiensis	both	leaf-like	spirodistichous	pubescent, glabrescent	clasping	20-45	equal	no	absent	obscure or absent
Morelotia gahniiformis	both	leaf-like	spirodistichous	glabrous	loose	25-39	yes	yes	absent	obscure or absent
Morelotia involuta	both	leaf-like	spirodistichous	glabrous	loose	26-38	yes	no	absent	obscure or absent
Morelotia microcarpa	both	leaf-like	spirodistichous	glabrous	clasping	8-30	equal	yes	absent	present
Morelotia octandra	both	leaf-like	spirodistichous	glabrous	clasping	18-35	equal	yes	absent	obscure or absent
Tetraria	basal or both	leaf-like	spirodistichous	glabrous	loose to clasping	18-82(-92)	yes or no	yes or no	absent	obscure or absent
Tetraria arundinacea	both	leaf-like	spirodistichous	glabrous	clasping	45-65	no	yes	absent	obscure or absent
Tetraria capillacea	both	leaf-like	spirodistichous	glabrous	clasping	18-82	yes	no	absent	obscure or absent
Tetraria cernuua	basal or both	leaf-like	spirodistichous	glabrous	loose to clasping	25-60(-92)	equal	no	absent	obscure or absent
Tetraria thermalis	both	leaf-like	spirodistichous	glabrous	clasping	52-80	no	yes	absent	obscure or absent

(*Continued...*)

Character	**Leaves**			**Leaf sheath**						
Name	basal / cauline / both	bract- / leaf-like at base	spirotristichous / spirodistichous	body glabrous / scabrous / other	loose / clasping	length (mm)	broader than blade: Y/N	margin below blade hairy: Y/N	ligule: P/A	pseudopetiole: P/A
Tricostularia	basal or both	bract-like	spirodistichous	glabrous	clasping, rarely loose	9-100	yes	yes or no	absent	obscure, absent or obvious
Tricostularia aphylla	both	bract-like	spirodistichous	glabrous	clasping	16-31	yes	yes	absent	obscure or absent
Tricostularia bennettiana	both	bract-like	spirodistichous	glabrous	clasping	16-28	yes	yes	absent	obscure or absent
Tricostularia compressa	basal	bract-like	spirodistichous	glabrous	clasping	9-44	yes	no	absent	obscure or absent
Tricostularia davisii	both	bract-like	spirodistichous	glabrous	clasping	13-25	yes	yes	absent	obscure or absent
Tricostularia drummondii	both	bract-like	spirodistichous	glabrous	clasping	?	yes	?	absent	obscure or absent
Tricostularia exsul	both	bract-like	spirodistichous	glabrous	clasping	33-80	yes	yes	absent	obscure or absent
Tricostularia lepschii	basal	bract-like	spirodistichous	glabrous	clasping	14-59	yes	no	absent	obscure or obvious
Tricostularia neesii	both	bract-like	spirodistichous	glabrous	clasping	12-100	yes	yes	absent	obscure or absent
Tricostularia newbeyi	both	bract-like	spirodistichous	glabrous	clasping	15-25	yes	yes (or no)	absent	obscure or absent
Tricostularia pauciflora	both	bract-like	spirodistichous	glabrous	clasping	11-17	yes	no	absent	obscure or absent
Tricostularia sandifordiana	both	bract-like	spirodistichous	glabrous	loose	9-21	yes	no	absent	obscure or absent
Tricostularia sp. Albany	both	bract-like	spirodistichous	glabrous	clasping	?	yes	?	absent	obscure or absent
Tricostularia sp. Mogumber	basal	bract-like	spirodistichous	glabrous	clasping	?	yes	?	absent	1-12.5
Tricostularia sp. Porongurup	both	bract-like	spirodistichous	glabrous	clasping	?	yes	?	absent	obscure or absent
Tricostularia sp. Two Peoples Bay	both	bract-like	spirodistichous	glabrous	clasping	?	yes	no	absent	obscure or absent
Xyroshoenus hornei	both	leaf-like	spirodistichous	scabrous	loose	30-60	yes	no	absent	obscure or absent

(*Continued...*)

Character	**Leaf blade**							
Name	lower leaf length (cm)	lower leaf width (mm)	linear / attenuate	section	margin entire / other	margin hairy: Y/N	midrib hairy: Y/N	apex shape
Ammothryon grandiflorum	(15–)22–46	5–15	linear	flat or folded	entire	yes	yes	attenuate
Chaetospora	4-21	0.3-0.9	linear	flat to canaliculate to involute and appearing terete	entire or serrulate	yes	no	long-attenuate
Chaetospora curvifolia	5–20	0.3-0.9	linear	flat to canaliculate	entire	yes	no	long-attenuate
Chaetospora subbulbosa	4-15	0.3-0.7	linear	flat to canaliculate, slighty involute`	entire	yes	no	long-attenuate
Chaetospora turbinata	6-21	0.3-0.7	linear	canaliculate to involute, appearing terete	serrulate	yes	no	long-attenuate
Morelotia	12-62	2-8	linear	flat, channeled or revolute	entire	yes	yes or no	long-attenuate
Morelotia affinis	20-62	4-8	linear	flat, involute and appearing terete with age	?serrulate	yes	yes	long-attenuate
Morelotia australiensis	12-18	2-6	linear	channelled to flat	entire	yes	yes	long-attenuate
Morelotia gahniiformis	15-45	2-8	linear	flat, involute and appearing terete with age	?serrulate	yes	no	long-attenuate
Morelotia involuta	20-60	2.5-4	linear	flat, involute and appearing terete with age	entire	yes	no	long-attenuate
Morelotia microcarpa	16-38(-60)	2-2.5	linear	flat or complicate, margins often recurved	entire	yes	no	long-attenuate
Morelotia octandra	15-60	2-4	linear	revolute	entire	yes	no	long-attenuate
Tetraria	6-100	0.5-24	linear	flat to involute and appearing terete, or V-shaped	denticulate or entire	yes	no	long-attenuate
Tetraria arundinacea	40-100	5-10	linear	V-shaped	denticulate	yes	no	long-attenuate
Tetraria capillacea	12-48(-75)	0.5-0.7	linear	V-shaped, margins flat to involute	entire	yes	no	setaceous

(*Continued...*)

Character	**Leaf blade**							
Name	lower leaf length (cm)	lower leaf width (mm)	linear / attenuate	section	margin entire / other	margin hairy: Y/N	midrib hairy: Y/N	apex shape
Tetraria cernuua	6-25	1.1-2.0	linear	flat to lunate, incurved and appearing terete with age	entire	yes	no	long-attenuate
Tetraria thermalis	17-40(-80)	10-24	linear	flat to broadly V-shaped	entire	yes	no	long-attenuate
Tricostularia	0-12.5	0.1-1.1	linear or triangular	flat to channelled	entire	yes or no	no	long-attenuate or acute
Tricostularia aphylla	0.6-1.5(-2.4)	0.7-1.1	linear	flat to channelled	entire	yes	no	long-attenuate
Tricostularia bennettiana	0.1-0.3	0.05	linear	flat	entire	yes	no	long-attenuate
Tricostularia compressa	0-0.1	0.3	triangular	flat	entire	no	no	acute
Tricostularia davisii	0.3-1.0	0.1-0.3	linear	flat	entire	yes	yes	long-attenuate, setaceous
Tricostularia drummondii	1-5(-8)	?	linear	flat	entire	?	?	long-attenuate
Tricostularia exsul	0.1-0.2	0.4-0.6	linear	flat	entire	yes	no	acute
Tricostularia lepschii	0.25-0.35	0.25-0.35	linear	flat	entire	yes	no	long-attenuate to acute
Tricostularia neesii	0.3-0.5	0.2-0.4	linear	flat	entire	yes or no	no	attenuate
Tricostularia newbeyi	0.1-0.2	0.05	triangular	flat	entire	yes	no	acute
Tricostularia pauciflora	0.5-6(-7)	0.3-0.7	linear	channelled	entire	no	no	long-attenuate
Tricostularia sandifordiana	0.6-1.1	0.6-0.9	linear	channelled	entire	yes	no	long-attenuate
Tricostularia sp. Albany	1-3	?	linear	flat	entire	?	?	?
Tricostularia sp. Mogumber	c. 0.3-0.5	?	linear	flat	entire	?	?	?
Tricostularia sp. Porongurup	1-12.5	?	linear	?	entire	?	?	?
Tricostularia sp. Two Peoples Bay	c. 0.3-0.5	?	linear	flat	entire	?	?	?
Xyroshoenus hornei	50-90	(5-)10-15	linear	flat, revolute with age	denticulate	yes	yes	long-attenuate

(*Continued...*)

Character	**Inflorescence**													
Name	form	shape in outline	length (cm)	width / diam. (mm)	Length ratio relative to diam. (min to max)	no. nodes	bracts: bract- / leaf-like	bracts > / = / < branchlets (can = spikelet clusters)	branches spreading / other	basal lateral branch length (mm)	spikelet no./ lateral branchlet	peduncle length below spikelet (mm)	spikelet prophyll: P/A	spikelet prophyll length
Ammothryon grandiflorum	open panicle-like	narrow	12–75	20–45	6-17	8-15	leaf-like	exceeding	spreading	45-75	(1–)3–12	7–16	absent	n/a
Chaetospora	head-like or elongate head-like	subglobular, obovate or turbinate	0.5-1.7	6-16	0.8-1.1	2-6	leaf-like	exceeding	compact, hidden	4.5-6.6	(1)2-5	0.1-1.4	present	1.1-3.8
Chaetospora curvifolia	head-like	subglobular	0.5-1.2	7-15	0.7-0.8	2-6	leaf-like	exceeding	compact, hidden	4.5-6.1	3-5	0.1-0.5	present	3.8
Chaetospora subbulbosa	head-like	subglobular	0.6-1.3	9-16	0.7-0.8	3-6	leaf-like	exceeding	compact, hidden	5.1-6.6	3-5	0.2-1.4	present	1.1
Chaetospora turbinata	elongate head	obovate to turbinate	0.6-1.7	6-10	1-1.7	2-4	leaf-like	exceeding	compact, hidden	5.9-6.3	2-4	0.4-0.8	present	3.1
Morelotia	open or dense panicle-like	linear to lanceolate	5-35	5-35	3.3-21(-25)	3-8	leaf-like	shorter to exceeding	erect	20-70	2-20	0.5-5	present	1.4-13
Morelotia affinis	dense panicle-like	linear	5-30	15-35	3.3-8.5	5-8	leaf-like	exceeding	erect	20-70	3-15	0.5-1	present	1.4-1.6
Morelotia australiensis	open panicle-like	linear	15-27	10-20	15-13.5	3-5	leaf-like	shorter to equal	erect	30-45	3-10	1-2	present	3.7-4.1
Morelotia gahniiformis	dense panicle-like	linear	(5-)10-35	10-25	(5-)10-14	3-7	leaf-like	exceeding	erect	35-65	2-8	0.5-2	present	2.1-2.5
Morelotia involuta	dense panicle-like	linear	10.5-21	5-10	c. 21	5-8	leaf-like	exceeding	erect	20-25	(1)2 or 3	0.5-3	present	5.3-6.3
Morelotia microcarpa	subspiciform panicle-like	linear	6-15(-25)	7-10	8.5-15(-25)	5-7	leaf-like	exceeding	erect	8-40	12-20	0.5-3	present	3.3-3.8
Morelotia octandra	open panicle-like	linear to lanceolate	13-35	10-20	13-17.5	4-7	leaf-like	equal to exceeding	erect	25-45	10-16	0.5-5	present	5.3-13
Tetraria	elongate panicle-like	linear to lanceolate	6-80	1.5-100	0.7-17	1-11	leaf-like at base and bract-like above	shorter to exceeding	erect, spreading, or arcuate	2.5-200	1-6	0.5-15	present	1.3-23.5
Tetraria arundinacea	elongate panicle-like	lanceolate	30-70	50-100	6-0.7	6-11	leaf-like at base and bract-like above	shorter	erect to spreading	70-200	2-6	0.5-4.5	present	1.3-2.6
Tetraria capillacea	elongate panicle-like	linear	6-25	8-15	7.5-17	4-7(-10)	leaf-like at base and bract-like above	exceeding	erect	46-85	3-5	0.5-15	present	3.6-4.4
Tetraria cernuua	elongate panicle-like	linear	6-28	15-80	4-3.5	1-4	leaf-like at base and bract-like above	equal to exceeding	arcuate	25-40	1-2	0-2.5	present	2.4-3.3
Tetraria thermalis	elongate or contracted panicle-like	lanceolate	17-80	25-50	7-16	(5-)6-10	leaf-like	equal to exceeding	erect	35-70	2-6	1-3.5	present	19-23.5
Tricostularia	slender or contracted panicle-like or subcapitate	linear, to oblate	0.7-12	3-17	1.7-20	0-9	bract-like, rarely almost pungent	shorter to exceeding	erect	0-29	1-7	0.2-4	present	0.6-10.6

(*Continued...*)

Character	**Inflorescence**													
Name	form	shape in outline	length (cm)	width / diam. (mm)	Length ratio relative to diam. (min to max)	no. nodes	bracts: bract- / leaf-like	bracts > / = / < branchlets (can = spikelet clusters)	branches spreading / other	basal lateral branch length (mm)	spikelet no./ lateral branchlet	peduncle length below spikelet (mm)	spikelet prophyll: P/A	spikelet prophyll length
Tricostularia aphylla	slender panicle-like	linear	4.5-9	3-9	15-10	4-9	bract-like	shorter	erect	10-26	(2-)3-7	1.5-4	present	3.9-5.5
Tricostularia bennettiana	contracted panicle-like	linear	1.5-3.5	5-8	3-4.4	2-4	bract-like	exceeding	erect	5-7	1-3	0.5-1	present	5-6.5
Tricostularia compressa	contracted panicle-like	narrow-oblate	1.5-3.2	4-7	3.7-5	2-4	bract-like	shorter	erect	5-9	3-5	1	present	1.7-2.4
Tricostularia davisii	contracted panicle-like (subcapitate)	obconical to obovate	0.7-1.5	3-5	2.3-4.4	3-5	bract-like, sometimes almost pungent	exceeding	erect	5-11	1-2	0.2-0.8	present	0.6-0.9
Tricostularia drummondii	slender panicle-like	linear m/less	3-4(-7)	c. 3-5	c. 4	5-6	bract-like	exceeding	erect	c. 15	2-3	?	present	?
Tricostularia exsul	elongate panicle-like-like	linear	8-12	4-9	20-13.3	5-9	bract-like	equal	erect	20-29	3-7	1-3	present	9.5-13
Tricostularia lepschii	contracted panicle-like	subglobular to ovate	0.7-1.1	4-8	1.7-1.4	1-2(-3)	bract-like	shorter to equal	erect	4-6	2-4	0.5-1	present	4-4.8
Tricostularia neesii	contracted panicle-like	narrow-oblate to lanceolate	1.5-2.2	4-6	3.7-4	2-4	bract-like	exceeding	erect	10-15	1-2	0.1-0.5	present	4.0-6.1
Tricostularia newbeyi	slender panicle-like	linear	1.5-6	5-8	3-7.5	6-9	bract-like	shorter	erect	7-12	(1-)2-4	0.5-1.5	present	3.7-5
Tricostularia pauciflora	contracted panicle-like	oblate	0.8-1.5	5-8	1.6-1.9	0 or 1	bract-like	shorter	erect	n/a	1-3	1-3	present	3.6-5.5
Tricostularia sandifordiana	contracted panicle-like	oblate to lanceolate	1.7-4.5	10-17	1.7-2.6	0-1	bract-like	shorter	erect	8-12	2-5	1-3.5	present	7.6-10.6
Tricostularia sp. Albany	elongate panicle-like-like	linear, with disjunct, sterile lowest node	4-8	2-3	2-2.7	5-6	bract-like	exceeding to equalling	erect	?	?	?	present	?
Tricostularia sp. Mogumber	sub-capitate	obconical / obovate in outline	c. 1	?	<2	?0-1	bract-like	shorter	erect	?	?	?	present	?
Tricostularia sp. Porongurup	slender panicle-like	linear	c. 8-15	c. 5	16-40	c. 8-12	bract-like	shorter	erect	?	?	?	present	?
Tricostularia sp. Two Peoples Bay	elongate panicle-like-like	linear	(6-)8-12	c. 2	(3-)4-6	5-7	bract-like	shorter or equal	erect	?	?	?	present	?
Xyroshoenus hornei	open panicle-like	lanceolate to ovate	45-60	100-350	4.5-1.7	8-12	leaf-like	shorter	arcuate	80-250	1	3-8	present	1.5-2.2

(*Continued...*)

Character	**Spikelets**											
Name	glume colour	shape in outline	length (mm)	width (mm)	no. glumes	no. fertile	upper flower fertility	2nd flower fertility	3rd flower fertility	4th flower fertility	basal glume length	fertile glume indumentum
Ammothryon grandiflorum	brown	narrow-ovate	12–22	2.2-2.6	10–14	2–4	bisexual fertile	bisexual fertile	bisexual fertile	bisexual fertile	3-6	hairy, glabrescent
Chaetospora	pale to dark brown or chestnut	narrow-ovate	4.7-8	1.2-3.2	5-9	1-3	bisexual fertile	functionally male or sterile	functionally male or sterile	n/a	2.6-4.5	puberulent or glabrous
Chaetospora curvifolia	dark brown to black	narrow-ovate	4.7-6.9	1.9-2.7	5-8	1-2	bisexual fertile	functionally male or sterile	n/a	n/a	2.8	puberulent or glabrous
Chaetospora subbulbosa	pale brown	narrow-ovate	5-8	1.2-1.8	6-8	3	bisexual fertile	functionally male or sterile	functionally male or sterile	n/a	2.6	puberulent
Chaetospora turbinata	pale red-brown to chestnut brown	narrow-ovoid to oblong-ovoid or compressed	5.5-8.0	1.9-3.2	5-9	1	bisexual fertile	n/a	n/a	n/a	4.5	puberulent
Morelotia	pale to brown to dark brown or chestnut	lanceolate to ovate	6.5-15	0.9-3.1	5-8(-9)	1-2	bisexual fertile, infertile or male sterile	bisexual fertile or bisexual sterile or male fertile	bisexual fertile or absent	n/a	2.5-7.8	glabrous, scabrous or pubescent
Morelotia affinis	reddish brown	narrow-lanceolate to ovate-lanceolate	6.5-10	1.4-2.2	7	2	infertile	functionally male	bisexual fertile	n/a	2.8	puberulent
Morelotia australiensis	pale brown	narrow-ovate	8-10	1.8-2.3	5	2	bisexual fertile	bisexual sterile or ?male fertile	n/a	n/a	6-7	glabrous
Morelotia gahniiformis	brown	narrow-ovate	8-10	2-3	6-8	2	infertile	functionally male	bisexual fertile	n/a	3.8-4.1	hispidulous
Morelotia involuta	brown	lanceolate	7-9	1.3-1.5	7	1	infertile	bisexual fertile	n/a	n/a	4	glabrous
Morelotia microcarpa	dark brown	lanceolate	3.5-4	0.9-1.1	6	3	bisexual fertile	bisexual sterile	bisexual sterile	n/a	1.2-2.2	scabrous
Morelotia octandra	chestnut to brown	ovate	10-15	2-3.1	7(9)	2	male sterile	bisexual fertile	n/a	n/a	5.0-7.8	scabrous to pubescent
Tetraria	pale to dark brown	elliptic to ovate	4.7-25	1.1-3.6	5-9	2-3	bisexual fertile	bisexual fertile or functionally male	functionally male or absent	n/a	1.1-15	glabrous or puberulent, or margins scabrid
Tetraria arundinacea	brown	oblate to lanceolate	4.7-6.6	1.2-1.8	6-9	2	bisexual fertile	bisexual fertile	n/a	n/a	1.1-1.9	glabrous but margins ciliate
Tetraria capillacea	brown	elliptic to lanceolate	5.5-10.5	1.5-2	5-9	2(-3)	bisexual fertile	bisexual fertile or functionally male	functionally male or absent	n/a	2.2-2.8	glabrous but margins ciliate
Tetraria cernuua	pale brown to red-brown	elliptic	8-15	1.1-2.0	(8)9	2	bisexual fertile	funtionally male	n/a	n/a	2.8-3.1	glabrous
Tetraria thermalis	brown to dark brown	ovate	16-25	2.2-3.6	8-9	3	bisexual fertile	bisexual fertile or functionally male	functionally male	n/a	12-15	puberulous above, margins glabrous to ciliate

(*Continued...*)

Character	**Spikelets**											
Name	glume colour	shape in outline	length (mm)	width (mm)	no. glumes	no. fertile	upper flower fertility	2nd flower fertility	3rd flower fertility	4th flower fertility	basal glume length	fertile glume indumentum
Tricostularia	brown	lanceolate to oblate	2.8-11	0.9-3.4	4-7(-9)	2-3	bisexual fertile	male fertile	male fertile or absent	n/a	1.4-4.5	glabrous, margins and keel ciliate or scabrous
Tricostularia aphylla	brown	lanceolate	4.7-7.2	1.7-2.4	(5-)7	2 or 3	bisexual fertile	male fertile	male fertile or absent	n/a	2.7-3.1	glabrous (margin finely ciliate)
Tricostularia bennettiana	reddish brown	lanceolate	4-6	1.5-1.8	5-6	2	bisexual fertile	bisexual fertile	n/a	n/a	2.2-2.7	scabrous on keel and margins
Tricostularia compressa	brown	oblate	2.8-5.1	0.9-1.6	4-5	2	bisexual fertile	male fertile	n/a	n/a	1.4-2.3	glabrous
Tricostularia davisii	brown	lanceolate	3.7-5.1	0.9-1.1	6	2	bisexual fertile	male fertile	n/a	n/a	2.9-4.2	ciliate on keel and margins
Tricostularia drummondii	?	lanceolate	?	?	?	?2	bisexual fertile	?	?n/a	n/a	?	glabrous
Tricostularia exsul	brown	lanceolate	8.5-11	2.1-3.3	5-6	3	bisexual fertile	male fertile	male sterile	n/a	3.6-4.2	scabrous on keel and margins
Tricostularia lepschii	brown	lanceolate	4-6	1.2-1.3	6	2	bisexual fertile	bisexual fertile or functionally male	n/a	n/a	1.5-3	glabrous (keel scabrous)
Tricostularia neesii	brown	lanceolate	5.5-6.8	1.1-1.7	5-6	2	bisexual fertile	male fertile	n/a	n/a	3.6-4.5	ciliate on keel and margins
Tricostularia newbeyi	pale brown to brown	lanceolate	4.4-5.6	1.3-1.8	6-7	2	bisexual fertile	bisexual fertile or functionally male	n/a	n/a	2.9-3.4	glabrous (keel & marigins scabrous)
Tricostularia pauciflora	brown	lanceolate	4-6	1.7-3	5 or 6	2 or 3	bisexual fertile	male fertile	male fertile or absent	n/a	2.5-3.5	glabrous (keel scabrous)
Tricostularia sandifordiana	brown	lanceolate	8-10	1.4-2.0	7(+2)	2	bisexual fertile	male fertile	n/a	n/a	1.6-2.1	glabrous (keel & marigins scabrous)
Tricostularia sp. Albany	mid yellow-brown to mid red-brown near apex	lanceolate	?	?	?	?2	bisexual fertile	?	?n/a	n/a	?	?
Tricostularia sp. Mogumber	pale brown to brown	lanceolate	?	?	?	?2	bisexual fertile	?	?n/a	n/a	?	?
Tricostularia sp. Porongurup	dark brown	lanceolate	'large'	?	?	?2	bisexual fertile	?	?n/a	n/a	?	?
Tricostularia sp. Two Peoples Bay	mid yellow-red brown	lanceolate	?	?	?	?2	bisexual fertile	?	?n/a	n/a	?	glabrous
Xyroshoenus hornei	brown to dark brown	oblate to lanceolate	5-8	1.5-2	7-9	2	bisexual fertile	male fertile	n/a	n/a	2.5	hispidulous

(*Continued...*)

Character											
Name	fertile glume apex	fertile glume length (mm)	fertile glume width (mm)	mucro length (mm)	rachilla compact / elongate	rachilla sinuous: Y/N	perianth: P/A	# perianth segments	perianth length (mm)	perianth shape	perianth indumentum
Ammothryon grandiflorum	acute	11-20	2-2.4	3.9-4.5	compact	not or scarsely	absent	n/a	n/a	n/a	n/a
Chaetospora	acute to acuminate	3.8-6.0	0.9-1.6	0.3-1.5	compact	no	present	6	0.2-2.0	flat or compressed to bristle-like	margins glabrous, ciliate or plumaose
Chaetospora curvifolia	acute to acuminate	4.2-5.9	1.1-1.3	1.1-1.5	compact	no	present	6	1.5-2.0	flat	margins ciliate
Chaetospora subbulbosa	acute to acuminate	3.8-6.0	0.9-1.4	0.3-0.9	compact	no	present	6	0.2-0.4	compressed to terete	glabrous or margins ciliate
Chaetospora turbinata	acute to acuminate	4.5-6.0	1.1-1.6	0.6-1.2	compact	no	present	6	1.2-2.0	compressed to bristle-like	plumose
Morelotia	obtuse or acute to acuminate	4.5-11.5	1.6-3.4	0.4-3.0	compact or fruiting internode elongate	once or no	absent or present	0, 2 or 6	0.4-1.5	filiform	glabrous
Morelotia affinis	acuminate to acute	4.5-9.0	1.8-3.4	0.4	fruiting internode elongate and curved	once	absent	n/a	n/a	n/a	n/a
Morelotia australiensis	acute to obtuse	6-9	1.6-2.1	1.5	compact	no	absent	n/a	n/a	n/a	n/a
Morelotia gahniiformis	acuminate to acute	5.6-9.9	1.8-3.4	1.5	fruiting internode elongate and curved	once	absent	n/a	n/a	n/a	n/a
Morelotia involuta	acuminate	8-9	1.7-2.1	3.0	compact	no	present	6	0.4-1.1	filiform	glabrous
Morelotia microcarpa	acute to acuminate	2.6-3.4	0.7-0.9	3.0	compact	no	absent or present	2	1-1.5	compressed	glabrous
Morelotia octandra	acute to acuminate	7.2-11.5	1.8-2.9	0.5-1.0	compact	shortly around fruit	absent	n/a	n/a	n/a	n/a
Tetraria	acute to long-acuminate	4.1-15	0.8-3.5	0-12	compact	no	absent or present	0 or 6	0.4-5	filiform or subulate or absent	glabrous, scabrid or plumose
Tetraria arundinacea	subacute	4.1-5.3	1.1-1.7	0.5	compact	no	present	6	3.3-4.4	filiform	densely scabrous
Tetraria capillacea	acute	6.0-8.5	0.8-1.6	0.7	compact	no	absent or present	0 or 6	0.4-0.6	filiform	glabrous to minutely scrabrid, margins minutely ciliate
Tetraria cernuua	acute to acuminate	8.5-12	1.1-1.5	0	compact	no	?absent	n/a	n/a	n/a	n/a

(*Continued...*)

Character											
Name	fertile glume apex	fertile glume length (mm)	fertile glume width (mm)	mucro length (mm)	rachilla compact / elongate	rachilla sinuous: Y/N	perianth: P/A	# perianth segments	perianth length (mm)	perianth shape	perianth indumentum
Tetraria thermalis	long-acuminate	12-15	2.1-3.5	5-12	compact	no	present	6	3-5	subulate	plumose
Tricostularia	obtuse or acute to acuminate	2.9-9.8	0.7-2.8	0-1.2	compact	no	present	6	0.2-1.2	flattened to subulate	glabrous or margins ciliate
Tricostularia aphylla	acute	4.5-7.0	1.5-2.2	0	compact	no	present	6	0.8-1.0	flattened, narrowly triangular	margins ciliate
Tricostularia bennettiana	acuminate	3.7-4.9	1.3-1.6	0.7	compact	no	present	6	0.6-1	filiform	a few minute hairs at apex
Tricostularia compressa	obtuse to acute	3.3-4.1	0.8-1.1	0	compact	no	present	6	0.3-0.9	subulate	glabrous
Tricostularia davisii	acuminate	3.2-4.2	0.7-0.9	0.2-0.6	compact	no	present	6	0.4-0.6	subulate	glabrous or minutely hispid at apex
Tricostularia drummondii	acuminate	c. 3	?	0.2-0.3	compact	no	present	6	?	?	?
Tricostularia exsul	acuminate	7.0-8.8	1.3-2.2	0.3-1.0	compact	no	present	6	0.7-2.0	filiform	scabrous
Tricostularia lepschii	acute to acuminate	4-4.5	1-1.1	0.6	compact	no	present	6	0.4-1.1	compressed to filiform	a few minute hairs at apex
Tricostularia neesii	acuminate	4.7-5.8	0.9-1.3	0.6-1.2	compact	no	present	6	0.5-1.2	filiform	a few minute hairs at apex
Tricostularia newbeyi	acuminate	3.5-5	1.1-1.6	0.8	compact	no	present	6	0.5-1.1	filiform	a few minute hairs at apex
Tricostularia pauciflora	acute to acuminate	2.9-4.0	1.5-2.8	0.5	compact	no	present	6	0.2-0.8	flattened	glabrous
Tricostularia sandifordiana	acute	6.3-9.8	1.5-2.8	0-0.5	compact	no	present	6	0.6	flattened	glabrous
Tricostularia sp. Albany	acuminate	c. 5	?	c. 0.2	compact	no	?	?	?	?	glabrous
Tricostularia sp. Mogumber	acuminate?	?	?	?	compact	no	?	?	?	?	?
Tricostularia sp. Porongurup	acuminate?	?	?	?	compact	no	?	?	?	?	?
Tricostularia sp. Two Peoples Bay	acuminate	6-7	?	0.1-0.2	compact	no	?	?	?	?	sparsely minutely ciliolate; otherwise glabrous
Xyroshoenus hornei	cuspidate	5-6	1.8-2.6	0	elongate	sinuous around fruit	present	(6-)7-8)	5-6	flattened	long plumose

(*Continued...*)

Character	**Stamens**							
Name	no.	connective length (mm)	connective shape	connective persistent on nut: Y/N	anther colour	anther length (mm)	anther appendage length (mm)	anther appendage indumentum
Ammothryon grandiflorum	3	6–11	linear to subulate	no	pale yellow	7–10	1.0–1.5	glabrous
Chaetospora	3	2.0-6.2	linear to subulate	no	yellow	1.8-3.1	0.5-0.8	glabrous
Chaetospora curvifolia	3	2.6-4.5	linear to subulate	no	yellow	2.0-2.5	0.5-0.7	glabrous
Chaetospora subbulbosa	3	2.0-3.5	linear to subulate	no	yellow	2.3-3.1	0.6-0.8	glabrous
Chaetospora turbinata	3	4.4-6.2	linear to subulate	no	yellow	1.8.2.5	0.5-0.6	glabrous
Morelotia	3, 6 or 8	1.8-9.6	linear	yes or no	yellow or pale yellow	3.1-6.5	0.5-2.0	glabrous or scaberulous
Morelotia affinis	3	6.3-8.8	linear	yes	yellow	3.6-4.2	1.4	glabrous
Morelotia australiensis	(3)6	5-7	linear	no	yellow	5.5-6.5	1.0	scaberulous
Morelotia gahniiformis	3	4.3-9.6	linear	yes	yellow	3.1-4.2	0.5	scaberulous
Morelotia involuta	3	5.1-6.8	linear	yes	pale yellow	4-5	2.0	glabrous
Morelotia microcarpa	3	1.8-2.5	subulate	no	yellow	0.8-0.9	0.2	glabrous
Morelotia octandra	(4, 6)8(9)	5.3-8.4	linear	no	pale yellow	4.4-6.2	1.4	glabrous
Tetraria	3	3.4-16	subulate	no	yellow	2.3-3.8	0.4-1.1	glabrous or scaberulous
Tetraria arundinacea	3	3.4-3.9	subulate	no	yellow	2.3-2.7	0.4	glabrous
Tetraria capillacea	3	5.1-7.5	subulate	no	yellow	2.6-2.9	1.1	scaberulous
Tetraria cernuua	3	6.1-8.5	subulate	no	yellow	2.5	0.9	glabrous
Tetraria thermalis	3	12-16	subulate	no	yellow	3.4-3.8	0.7	glabrous
Tricostularia	3	2.3-6.9	subulate	no	yellow, pale yellow, cream	1.4-4.6	0.15-0.9	glabrous

(*Continued...*)

Character	**Stamens**							
Name	no.	connective length (mm)	connective shape	connective persistent on nut: Y/N	anther colour	anther length (mm)	anther appendage length (mm)	anther appendage indumentum
Tricostularia aphylla	3	5.1-6.9	subulate	no	pale yellow	2.0-4.0	0.2-0.5	glabrous
Tricostularia bennettiana	3	3.4-4.3	subulate	no	cream	2.6-3	0.5	glabrous
Tricostularia compressa	3	3.0-3.7	subulate	no	pale yellow	2.8-3.5	0.5	glabrous
Tricostularia davisii	3	3.3-4.6	subulate	no	cream	2.4-2.6	0.6-0.8	glabrous
Tricostularia drummondii	3	?	subulate	no	?	?	?	glabrous
Tricostularia exsul	3	5.9-7.8	subulate	no	yellow	3.6-4.1	0.8-1.2	glabrous
Tricostularia lepschii	3	unknown	subulate	no	unknown	1.5-2.2	0.3	glabrous
Tricostularia neesii	3	3.1-4.6	subulate	no	yellow	2.7-3.4	0.4-0.5	glabrous
Tricostularia newbeyi	3	4.1-5.5	subulate	no	yellow	2	0.3	glabrous
Tricostularia pauciflora	3	2.3-3.8	subulate	no	cream	1.4-1.6	0.15-0.2	glabrous
Tricostularia sandifordiana	3	3.1-3.6	subulate	no	yellow	4.2-4.6	0.9	glabrous
Tricostularia sp. Albany	?	?	?	?	?	c. 3	c. 0.5	glabrous
Tricostularia sp. Mogumber	?	?	?	?	?	?	?	?
Tricostularia sp. Porongurup	?	?	?	?	?	?	?	?
Tricostularia sp. Two Peoples Bay	?	?	?	?	?	?	?	?
Xyroshoenus hornei	3	4-6	subulate	no	yellow	3	0.8	scaberulous

(*Continued...*)

Character	**Style**						
Name	total length (mm)	base length (mm)	base enlarged: Y/N	base: glabrous / hairy	branch no.	branch length (mm)	branches: glabrous / hairy
Ammothryon grandiflorum	16–22	8–12	yes, slightly	glabrous	3	8–10	hairy
Chaetospora	3.5-5.6	1.4-3.5	no	glabrous	3	1.3-2.9	hairy
Chaetospora curvifolia	3.8-5.6	2.5-3.1	no	glabrous	3	1.3-2.5	hairy
Chaetospora subbulbosa	3.5-5.6	1.4-2.7	no	glabrous	3	2.1-2.9	hairy
Chaetospora turbinata	4.0-5.0	2.7-3.5	no	glabrous	3	1.3-1.5	hairy
Morelotia	7.0-15	3-7.3	yes or no	hairy or glabrous	3-5	2.5-10	hairy
Morelotia affinis	7.0-7.9	3.9-4.2	no	hairy	3	3.1-3.7	hairy
Morelotia australiensis	7.5-10	5-7	no	glabrous	3	2.5-3.0	hairy
Morelotia gahniiformis	7.1-8.0	4.6-5.1	no	hairy	3	2.5-2.9	hairy
Morelotia involuta	10-15	3-5	no	glabrous	3	7-10	hairy
Morelotia microcarpa	3.1-3.8	1.8-2.3	yes	glabrous	3	1.3-1.5	hairy
Morelotia octandra	8-10.5	5.5-7.3	yes	hairy	3-5	2.5-3.3	hairy
Tetraria	5.0-19	2.7-9	yes or no	hairy (at least partly)	3-4	1.6-10	hairy
Tetraria arundinacea	5.0-6.0	3.4-4.1	yes	hairy	3	1.6-1.9	hairy
Tetraria capillacea	6.7-8.1	4.8-5.6	no	hairy in upper half	3	1.9-2.5	hairy
Tetraria cernuua	6.6-7.4	2.7-3.1	no	hairy towards the apex	3	3.9-4.3	hairy
Tetraria thermalis	15.5-19	7.5-9	no	hairy	3-4	8-10	hairy
Tricostularia	2.0-6.4	0.5-3.5	no	hairy or glabrous	3	1.3-3.7	hairy
Tricostularia aphylla	4.6-6.4	1.9-2.7	no	glabrous	3	2.7-3.7	hairy
Tricostularia bennettiana	5.2-7.1	3.1-4.3	no	hairy towards the apical 1/3	3	2.1-2.8	hairy
Tricostularia compressa	2.7-3.6	1.4-1.7	no	glabrous	3	1.3-1.9	hairy
Tricostularia davisii	2.6-3.9	1.2-2.0	no	glabrous	3	1.4-1.9	hairy
Tricostularia drummondii	?	?	?	?	3	?	hairy
Tricostularia exsul	6.4-7.3	3.6-4.1	no	glabrous	3	2.8-3.2	hairy
Tricostularia lepschii	unknown	unknown	unknown	unknown	3	unknown	hairy
Tricostularia neesii	5.4-6.3	3.0-3.5	no	glabrous	3	2.4-2.8	hairy
Tricostularia newbeyi	2.8-4	1.5-2.4	no	hairy towards the apical 1/3	3	1.3-1.6	hairy
Tricostularia pauciflora	2.0-3.2	0.5-1.2	no	glabrous	3	1.5-2.0	hairy
Tricostularia sandifordiana	4.4-6.1	2.3-3.2	no (scarcely)	hairy towards the apical 1/3	3	2.1-2.9	hairy
Tricostularia sp. Albany	?	?	?	?	?	?	?
Tricostularia sp. Mogumber	?	?	?	?	?	?	?
Tricostularia sp. Porongurup	?	?	?	?	?	?	?
Tricostularia sp. Two Peoples Bay	?	?	?	?	?	?	?
Xyroshoenus hornei	10-13	5-6	no	glabrous	3	5-7	hairy

(*Continued...*)

Character	**Nutlet**												**Embryo**	**C_3 / C_4**
Name	sessile / stipitate	shape	length (mm)	diam. (mm)	rib no.	ribs [description]	indumentum on faces	face texture	face colour	apex shape	apex length (mm)	indumentum on apex	embryo type	C_3 / C_4
Ammothryon grandiflorum	?stipitate	subovoid	3.2–3.8	1.8–2.2	3	raised	glabrous	smooth	brown	conical	0.5	glabrous	?	C_3
Chaetospora	stipitate	obovoid to obpyriform	1.4-2.3	1.0-1.4	3	raised	glabrous	smooth or tuberculate	brown to dark brown, red-brown, or grey	cap-like to shortly conical	0-0.15	hairy or scabrous	Schoenus-type	C_3
Chaetospora curvifolia	stipitate	obovoid	1.4-1.7	1.0-1.1	3	raised	glabrous	smooth	dark brown	cap-like	0	hairy	?	C_3
Chaetospora subbulbosa	stipitate	obovoid	1.4-1.6	1.0-1.2	3	raised	glabrous	tuberculate	brown	cap-like to shortly conical	0.15	hairy	?	C_3
Chaetospora turbinata	stipitate	obpyriform to turbinate or obovoid	1.3-2.3	1.0-1.4	3	raised	glabrous	tuberculate at apex	grey to red-brown	cap-like	0	scabrous	Schoenus-type	C_3
Morelotia	sessile	ovoid to broad ellipsoid or globose	2.1-5.4	0.8-2.3	3-5	raised or impressed	glabrous	smooth	straw-coloured or red-brown to black	depressed-ovoid, broadly subconical to pyramidal	0.5-2.0	glabrous, scaberous or hispidulous	Schoenus-type	C_3
Morelotia affinis	sessile	elliptic-obloid	2.5-3.0	1.5	3	raised	glabrous	smooth	lustrous red-brown to black	subconical	0.9	glabrous	?	C_3
Morelotia australiensis	sessile	ovoid to ellipsoid	4.9-5.4	2.0-2.3	4-5	raised	glabrous	smooth	mid-brown	broadly subconical to pyramidal	1.4	hispidulous	?	?
Morelotia gahniiformis	sessile	ovate-ellipsoid to ellipsoid	2.7-3.0	2	3	impressed	glabrous	smooth	black, slightly glossy	trigonous-pyramidal	0.7	glabrous	Schoenus-type	C_3
Morelotia involuta	sessile	ellipsoid	2.1-2.7	0.8-1.0	3	raised	glabrous	smooth	straw-coloured	cylindric to trigonous pyramidal	0.5	glabrous	?	?
Morelotia microcarpa	stipitate	obovoid to globular	1.4-1.7	0.8-1.2	3	raised	glabrous	smooth	pale brown	pyramidal or conical	0.3	glabrous	?	?
Morelotia octandra	sessile	globose	4.5-5.1	1.6-1.8	3-5	raised	glabrous	smooth	pale brown	depressed-ovoid	1.5-2.0	scabrous-pubescent	?	C_3
Tetraria	stipitate	ovoid to broad ellipsoid	1.3-11	0.5-4.5	3-4	raised	glabrous	smooth or tuberculate	pale, mid, or dark brown	cap-like, shortly conical or shortly pyramidal	0-1.3	glabrous, puberulous or hispidulous	Schoenus-type	C_3
Tetraria arundinacea	stipitate	obovoid to ellipsoid	1.3-1.7	0.5-0.7	3	raised	glabrous	smooth	mid-brown	shortly conical	0.2	puberulous	?	C_3
Tetraria capillacea	stipitate	obovoid to ellipsoid	2.1-3.5	1.0-1.5	3	raised	glabrous	smooth	pale brown	shortly pyramidal	0.3-0.4	glabrous	Schoenus-type	?
Tetraria cernuua	stipitate	obloid to obovoid	1.8-2.9	1.2-1.4	3	raised	glabrous	tuberculate in upper third	pale brown	cap-like	0	hispidulous	?	C_3

(*Continued...*)

Character	**Nutlet**												**Embryo**	**C_3 / C_4**
Name	sessile / stipitate	shape	length (mm)	diam. (mm)	rib no.	ribs [description]	indumentum on faces	face texture	face colour	apex shape	apex length (mm)	indumentum on apex	embryo type	C_3 / C_4
Tetraria thermalis	stipitate	ovoid to broad ellipsoid	9-11	4.1-4.5	3-4	raised	glabrous	smooth	dark brown	cap-like to shortly conical	0-1.3	glabrous	Schoenus-type	?
Tricostularia	stipitate	obovoid to broad ellipsoid	1.2-2.5	0.8-1.5	3	raised	puberulous, hispidulous or glabrous	smooth	mid-brown or dark brown to almost black	cap-like or shortly conical	0-0.2	puberulous or hispidulous	?	C_3
Tricostularia aphylla	stipitate	obovoid to broad ellipsoid	2.2-2.4	1.3	3	raised	puberulous	smooth	mid-brown	cap-like	0	puberulous	?	C_3
Tricostularia bennettiana	stipitate	obovoid to obpyriform	1.2-1.5	0.8-0.9	3	raised	puberulous	smooth	mid-brown	shortly conical	0.2	puberulous	?	C_3
Tricostularia compressa	stipitate	ovoid	1.6-1.8	0.9-1.0	3	raised	hispidulous	smooth	mid-brown	cap-like	0	hispidulous	?	?
Tricostularia davisii	stipitate	obovoid to obpyriform or broad ellipsoid	1.2-1.7	0.8-1.0	3	raised	puberulous	smooth	dark brown to almost black	cap-like	0	puberulous	?	?
Tricostularia drummondii	stipitate	?	?	?	3	raised	puberulous	smooth	?	?	?	?	?	?
Tricostularia exsul	stipitate	broad ellipsoid	2.5-2.8	1.3-1.5	3	raised	puberulous	smooth	mid-brown to dark brown	shortly conical	0.2	puberulous	?	?
Tricostularia lepschii	stipitate	broad ellipsoid	2	1.3	3	raised	puberulous	smooth	mid-brown	cap-like	0	puberulous	?	?
Tricostularia neesii	stipitate	obovoid to obpyriform	1.9-2.2	0.8-1.0	3	raised	minutely puberulous	smooth	mid-brown	cap-like	0	puberulous	?	?
Tricostularia newbeyi	stipitate	obovoid to broad ellipsoid	1.8-2	1-1.3	3	raised	puberulous	smooth	mid-brown	cap-like	0.2	puberulous	?	?
Tricostularia pauciflora	stipitate	obovoid to obpyriform or broad ellipsoid	2.1-2.5	1.2-1.5	3	raised	puberulous	smooth	mid-brown to dark brown	shortly conical	0	puberulous	?	C_3
Tricostularia sandifordiana	stipitate	obovoid to obpyriform	1.7-2.1	0.8-1.1	3	raised	glabrous	smooth	mid-brown	cap-like	0.2	glabrous	?	?
Tricostularia sp. Albany	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tricostularia sp. Mogumber	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tricostularia sp. Porongurup	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tricostularia sp. Two Peoples Bay	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xyroshoenus hornei	sessile	subovoid	1.5-1.7	1	3	raised	glabrous	smooth	dark brown	cap-like	0.3	hispidulous	?	?

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Reassessment of the taxonomic status of Cyperaceae on Rapa Iti, Austral Islands, French Polynesia, with a new combination, *Morelotia involuta*

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Abstract

We reassess the current taxonomic status and distribution of Cyperaceae on Rapa Iti, Austral Islands, French Polynesia. This includes the poorly known *Machaerina involuta* H.St John (Cyperaceae, tribe Schoeneae), 86 years after it was first collected. Detailed morphological examination revealed that *M. involuta* belongs in *Morelotia* Gaudich., and the new combination, *Morelotia involuta* (H.St John) J.J.Bruhl & R.L.Barrett, is made here. Nineteen species of Cyperaceae are reported for Rapa Iti (10% of the vascular flora). The high diversity of Cyperaceae invites further discussion of the biogeographic connections and environmental conditions of Rapa Iti and a summary is provided. Notes on additional Cyperaceae named from Rapa Iti (*Carex rapaensis* (H.St John) K.L.Wilson, *Carex stokesii* F.Br., *C. stokesii* var. *aristata* F.Br., *Cyperus rapensis* F.Br., *Eleocharis caribaea* var. *stokesii* F.Br., *Gahnia stokesii* F.Br. and *Rhynchospora stokesii* F.Br.) are presented and a presently unidentified *Carex* is noted.

Keywords: Cyperaceae; *Machaerina*; *Morelotia*; Schoeneae; Hawaii; New Zealand; Pacific.

Introduction

A collaboration between Australia and French Polynesia has led to the reassessment of *Machaerina involuta* H.St John (Cyperaceae), 86 years after it was first collected on the remote island of Rapa Iti, Austral Islands. Surprisingly, the species remained unnamed for fifty years before being named by the collector of the type specimen, Harold St John (St John 1984). Jeremy Bruhl suspected that *M. involuta* was misplaced in that genus after examination of material at K. While reviewing generic relationships in the *Tricostularia* Nees ex Lehm. group of genera, we confirmed that *Machaerina involuta* is actually a species of *Morelotia* Gaudich. *Machaerina involuta* appeared to be only known from three collections made on a single expedition to Rapa Iti

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(Austral Islands, French Polynesia) in July 1934 by US botanists Harold St-John and F. Raymond Fosberg during the "Mangarevan expedition" funded by the Bernice Pauahi Bishop Museum of Honolulu, Hawai'i.

An enquiry was made by Russell Barrett to Jean-Yves Meyer as to whether any recent collections might have been made during more recent botanical expeditions. These include expeditions conducted by French botanists Jacques Florence (IRD, formerly known as ORSTOM) and Nicolas Hallé (Muséum national d'Histoire naturelle, Paris) in January–February 1984, and by a team of French Polynesian and US botanists (Délégation à la Recherche de la Polynésie française, New York Botanical Garden and National Tropical Botanical Garden, Kaua'i) in March–May and during a multidisciplinary scientific expedition to assess the terrestrial biodiversity of the Austral Islands led by Jean-Yves Meyer in December 2002 (see Meyer *et al.* 2014; Motley *et al.* 2014). While none was apparently known, Ravahere Taputuarai was recently undertaking botanical research on Rapa Iti, with no defined boat departure date due to COVID-19 travel restrictions.

Ravahere Taputuarai spent over three months on the island, February–June 2020. A targeted search for the species was therefore initiated, and at least seven populations were located. Subsequent searches of PAP and PTBG revealed that four collections had in fact been made during the 2002 expedition noted above, but they had initially been identified as Cyperaceae sp., *Carex* sp., or *Carex stokesii* F.Br., largely due to their dissimilarity to any *Machaerina* species (Chevillotte *et al.* 2019). The specimens, at PTBG, were later determined as the poorly known *Machaerina involuta* by Mark Strong (US; 2006), and confirmed by Tetsuo Koyama (MBK; 2010), but the specimens at PAP remained under their original determinations.

Rapa Iti (literally Little Rapa, to distinguish it from Easter Island or Rapa Nui, i.e. Big Rapa) is a small volcanic island (40 km^2) in the far south-east of the Austral Islands chain, some 1250 km south-southeast of Tahiti in the Pacific Ocean. The highest peak, Mont Perau or Perahu, is *c.* 650 m high. The island of Rapa Iti formed progressively between *c.* 4.1 and 4.8 Ma (Meyer and Claridge 2014a, 2014b). Annual rainfall is 2500–3800 mm, and year-round, allowing for the presence of rainforests and cloud forests at high elevation (Motley *et al.* 2014). Rapa Iti is one of only two Pacific islands with coal deposits, suggesting a long history of high vegetative productivity (Mueller-Dombois and Fosberg 1998). Rapa Iti has a significant history of human habitation, stretching back about 750 years (DiNapoli *et al.* 2018), with 515 inhabitants in 2017, and domestic livestock, especially goats, cattle, horses and pigs, have impacted the natural environment of the island (Prebble and Anderson 2012; Meyer *et al.* 2104, 2019). Uncontrolled fires are having an increasing impact on native vegetation, particularly through the promotion of introduced grasses (Meyer *et al.* 2014). Introduced plants, especially strawberry guava *Psidium cattleyanum* Sabine (Myrtaceae) and the thimbleberry *Rubus rosifolius* Sm. (Rosaceae), are also adding pressure to native remnant vegetation (Meyer *et al.* 2019). Rapa Iti and nearby Austral Islands are recognized by WWF to host several threatened endemic plant and animal species such as the Rapa fruit dove *Ptilinopus huttoni* and the Kuhl's lorikeet *Vini kuhlii*, only present in Rimatara (Zicus 2020). Many of the more than 60 endemic plant species are of conservation concern (Meyer and Claridge 2014a; Meyer *et al.* 2014).

The relatively young geological age, but often great isolation of Pacific islands makes for a very mixed flora of widespread, recently arrived species, and older chance dispersals that have led to subsequent speciation and relatively high local endemism (van Balgooy *et al.* 1996; Mueller-Dombois and Fosberg 1998; Kreft *et al.* 2008). Unfortunately, remoteness is negatively correlated with the impacts of invasive alien species (Moser *et al.* 2018).

The primary biogeographic connections, and therefore the biogeographic regionalisation of Rapa Iti and nearby islands have been the subject of much debate (see van Balgooy 1971; van Balgooy *et al.* 1996). Edwin B. Copeland (1873–1964), a US pteridologist with expertise on ferns in the Pacific islands, noted that Rapa appeared to be an exception to the general pattern of fern relationships where New Zealand origins were proposed for most Pacific species on the basis of morphological similarity, and a similar origin was postulated for most Cyperaceae in the Pacific (Copeland 1948). Rouhan *et al.* (2004, 2008), using phylogenetic analyses of relationships, showed that this was not true for the fern genus *Elaphoglossum* Schott ex J.Sm., but Viljoen *et al.* (2013) confirmed that an Austral origin is true for at least taxa in Cyperaceae tribe Schoeneae, with primary diversification taking place in Australia. Garnock-Jones (1976) established that *Veronica rapensis* F.Br. is most closely allied to New Zealand species.

Phylogenetic studies are now revealing both the potential origins and timing of dispersal events to remote Pacific islands (e.g. Price and Wagner 2018). Baldwin and Wood (2016) determined that the Rapa endemic genus *Apostates* Lander originated as a dispersal from North America, rather than being a radiation from Australia as suggested by its original description in the Australasian genus *Olearia* Moench. (see Lander 1989). Iwanycki Ahlstrand *et al.* (2019) found that two Rapa Iti endemic species of *Plantago* L. have their origins in North America, defying the usual pattern of proximity to major land masses, rather following the Pacific flyway for large marine birds. The expanded genus *Sclerotheca* A.DC. (Campanulaceae, now including *Apetahia* Baill.), endemic to South East Polynesia, appears to be sister to a Hawaiian radiation of lobelioids (Pillon *et al.* 2018).

Some authors are suggesting that the southern Austral Islands should be excluded from neighbouring biogeographic zones as their composition is a greater mix of both western (New Zealand, Australian), northern (Hawaiian, North American) and eastern (South American) connections than surrounding archipelagos (see Funk and Wood 2014; Zicus 2020). Florence (1997) and Meyer *et al.* (2014) recognise the Rapa group as distinct from the Austral Archipelago. Rapa in particular is unique in this region for having high, year-round rainfall, and lower temperatures compared to the nearest islands of the Austral and the Society Archipelagos. We here suggest that this first characteristic, combined with low species diversity (or 'taxonomic disharmony') typical of remote islands, high topographic diversity and highly fertile soils, offers significant opportunities for new arrivals to establish year-round (rather than in only seasonally suitable conditions). These combinations may be enough to explain the relatively high plant diversity and endemism on Rapa Iti compared with other islands in the region, including the high diversity of Cyperaceae.

Rapa Iti is host to 59 endemic plant species, out of a total of 191 (135 native) recorded species, the endemism rate of 31% is the highest rate in French Polynesia and Eastern Polynesia (Meyer *et al.* 2014). Endemic species continue to be described, such as *Melicope balgooyi* Appelhans, W.L.Wagner & K.R.Wood (Appelhans *et al.* 2014), *Bidens meyeri* V.A.Funk & K.R.Wood (Funk and Wood 2014) and *Pacifigeron indivisus* Saldivia (Saldivia *et al.* 2020).

Ten genera of flowering plants found on Rapa are endemic to the Pacific, seven of which are endemic to Eastern Polynesia, and three of these are endemic to Rapa Iti (Florence 1997; Meyer *et al.* 2014; Table 1). *Exocarpos* Labill. (Santalaceae) is widespread in Australia and New Caledonia (Kuijt 2015) and is here excluded from this list. *Geniostoma* J.R.Forst. & G.Forst. (Loganiaceae) has been re-circumscribed and includes species extending to Australia and the Indian Ocean (Gibbons *et al.* 2012). *Hebe* Comm. ex Juss. (Plantaginaceae) is now generally subsumed under a broadly circumscribed and monophyletic *Veronica* L. (Garnock-Jones *et al.* 2007). *Nesoluma* Baill. (Sapotaceae), is now included under *Sideroxylon* L. (Smedmark and Anderberg 2007). *Kadua* Cham. & Schltdl. (Rubiaceae) is endemic to the Pacific, its generic status having been supported by recent molecular phylogenetic data (Neupane *et al.* 2015; Gibbons 2020). *Morelotia* as traditionally circumscribed would also be added to the list of Pacific endemic genera found on Rapa (Table 1). However, the circumscription of *Morelotia* has recently been expanded to include three species from south-west Australia (Barrett *et al.* 2021). The flora of Rapa is quite dissimilar to that of nearby islands, sharing less than a quarter of its species with even the high volcanic islands of Raivavae, Rurutu and Tubuai, which have a more tropical climate than Rapa Iti (Meyer *et al.* 2014).

Table 1. List of Pacific Basin endemic angiosperm genera found on Rapa Iti.

Rapa Iti endemic genera	French Polynesian endemic genera	Eastern Polynesia endemic genera	Pacific endemic genera
Apostates (Asteraceae) *Metatrophis* (Urticaceae) *Pacifigeron* (Asteraceae)	*Haroldiella* (Urticaceae) *Oparanthus* (Asteraceae)	*Fitchia* (Asteraceae) *Sclerotheca* (formerly *Apetahia*, Campanulaceae)	*Corokia* (Argophyllaceae) [also one species in New South Wales, Australia] *Kadua* (Rubiaceae) *Meryta* (Araliaceae)

Cyperaceae on Rapa Iti

Cyperaceae (sedges) are commonly neglected components of ecosystems due to the challenges associated with identification and their often inconspicuous presence in the landscape. Ecosystem surveys commonly focus on dominants and common or showy species, and small or infertile species are easily overlooked, particularly when time-frames for surveys are limited. In remote locations, documentation of little-studied groups such as Cyperaceae remains an ongoing priority for research.

In Cyperaceae, whether species are local endemics or widespread appears to be correlated with the likelihood and mechanism of seed dispersal, which is partly correlated with the habitat, as discussed by Jacobs and Wilson (1996) for aquatic species (including Cyperaceae) in the Australasian region. Nineteen species of Cyperaceae have been collected on Rapa Iti (Table 2). Five species are highly localised in south-eastern Polynesia (three endemic to Rapa Iti), while the others have very broad distributions. Most of these have very small fruit, or are aquatic species, that are commonly dispersed by birds (Sorensen 1986; Bryson and Carter 1998; Cain *et al.* 2000).

Table 2. Cyperaceae recorded from Rapa Iti and their current status (based on Brown 1931; Meyer 2002; Meyer and Claridge 2014a; Sykes 2016; and specimens or images examined from B, BISH, BM, K, L, NY, P, PAP, PTBG, WAG and US). Alternative determinations are included to assist curation of herbarium specimens where only digital images were seen.

Current name	Native or Introduced	Endemic to Rapa	Type from Rapa
Carex rapaensis (H.St John) K.L.Wilson [some collections labelled as *Uncinia rapaensis*]	native	yes	*Uncinia rapaensis* H.St John
Carex stokesii F.Br.	native (Rapa, Rarotonga)	no	*Carex stokesii*; *C. stokesii* var. *aristata* F.Br.
Carex sp. (R.Taputuarai 861) [allied to *C. uncinata* L.f.]	native	unknown	
Cladium mariscus subsp. *jamaicense* (H.J.Crantz) Kük.	probably native but possibly introduced	no	
Cyperus brevifolius (Rottb.) Endl. ex Hassk. [some collections labelled as *Kyllingia brevifolia*]	uncertain	no	
Cyperus cyperinus (Retz.) Suringar [listed as *C. umbellatus* by Brown 1931]	introduced	no	
Cyperus cyperoides (L.) Kuntze	probably introduced but possibly native	no	
?*Cyperus ferax* Rich. [records by Brown 1931 at least partially based on sterile *Digitaria*; records may also refer to *Cyperus odoratus* L.]	?native	no	
Cyperus javanicus Houtt. [some collections labelled as *Mariscus javanicus*]	probably introduced but possibly native	no	
Cyperus mindorensis (Steud.) Huygh [collections labelled as *Kyllingia nemoralis*]	probably native	no	
Cyperus rapensis F.Br.	native (Rapa, Raivavae)	no	*Cyperus rapensis*
Eleocharis geniculata (L.) Roem. & Schult. [some collections labelled as *Eleocharis caribbaea* var. *stokesii*]	probably native but possibly introduced	no	*Eleocharis caribaea* var. *stokesii* F.Br.
Ficinia nodosa (Rottb.) Goetgh., Muasya & D.A.Simpson [some collections labelled as *Scirpus nodosus* or *Isolepis nodosus*]	native	no	
Fimbristylis dichotoma (L.) M.Vahl	native	no	
Gahnia aspera (R.Br.) Spreng. [some collections labelled as *Gahnia stokesii*]	native	no	*Gahnia stokesii* F.Br.
?*Isolepis levynsiana* (as *Cyperus tenellus* L.) [possibly confused with *Isolepis subtilissima*; *E.H.Quayle 352*, BISH; not examined]	probably introduced or an incorrect identification	no	
Isolepis subtilissima Boeckeler [some collections labelled as *Scirpus nodosus*]	probably native but possibly introduced	no	
Morelotia involuta (H.St John) J.J.Bruhl & R.L.Barrett [collections variously labelled as Cyperaceae sp., *Carex* sp., *Carex stokesii* or *Machaerina involuta*]	native	yes	*Machaerina involuta* H.St John
Rhynchospora stokesii F.Br. [some collections labelled as *Rhynchospora sclerioides* var. *stokesii* (F.Br.) Kük.]	native	yes	*Rhynchospora stokesii*; *R. stokesii* forma *saxicola* F.Br.
Schoenoplectus subulatus (Vahl) Lye [or recognised as *Schoenoplectus littoralis* subsp. *subulatus* (M.Vahl) T.Koyama]	probably native but possibly introduced	no	

Generic circumscription in Cyperaceae tribe Schoeneae has remained challenging due to very high levels of morphological variability (Bruhl 1995; Goetghebeur 1998), with resolution only being achieved recently through detailed molecular phylogenies (Zhang *et al.* 2004, 2007; Bruhl *et al.* 2008a, 2008b; Viljoen *et al.* 2013; Muasya 2016; Musili *et al.* 2017; Barrett *et al.* 2017, 2019; Semmouri *et al.* 2019). Considerable re-circumscription has been required in some genera (Wilson *et al.* 2012; Larridon *et. al.* 2018a, 2018b, 2019; Barrett *et al.* 2017, 2019, 2020).

Recognition and definition of both *Machaerina* Vahl and *Morelotia* Gaudich. has been debated for many years (Benl 1940a, 1940b; 1950; Kükenthal 1943; St John 1958; Kern 1962; Blake 1969; Bruhl 1995). Consensus has recently been reached, with *Machaerina* expanded to include *Baumea* Gaudich. and *Morelotia* accepted as a distinct genus from *Gahnia* J.R.Forst. & G.Forst. (Viljoen *et al.* 2013; Semmouri *et al.* 2019).

Larridon *et al.* (2018b) estimated that the *Tricostularia* Nees ex Lehm. clade originated around 28.4 (19.8–39.2) Ma. Viljoen *et al.* (2013) found that this clade likely originated in Australia, with the current distribution of genera and species outside Australia most likely due to long-distance dispersal events.

Methods

The description of *Morelotia involuta* is based on a specimen examined at NSW and specimen images available through online databases (indicated by *): Global Plants project on JSTOR, Consortium of Pacific Herbaria website, Naturalis, Australasian Virtual Herbarium, B, BISH, BM, K, NY, P, PAP and US.

Taxonomy

Morelotia Gaudich., *Voy. Uranie* 4(10): 416 (1829).

Type species: *Morelotia gahniiformis* Gaudich.

Kern (1962) considered *Morelotia affinis* and *M. gahniiformis* to belong in *Machaerina* based on the trigonous stems, revolute leaves, distichous glumes, presence of an imperfect second flower and greatly thickened style-base. This may have influenced St John's decision to describe his new species as *Machaerina involuta* (St John 1984), but no notes to this effect have been found. Morphological examination of the original collections and comparison with *Morelotia affinis* and *M. gahniiformis* confirm that *Machaerina involuta* also belongs in *Morelotia*. It appears to be closer in morphology to *M. affinis* than *M. gahniiformis*, but molecular data are yet to be obtained for *M. involuta* to confirm evolutionary relationships and estimate the age of divergence events. The three Pacific species of *Morelotia* are allied to three species from southern Western Australia that have historically been included in *Tetraria* (Barrett *et al.* 2021). The four geographic regions where *Morelotia* species occur are separated by distances of between 3950 and 7030km (Figure 1).

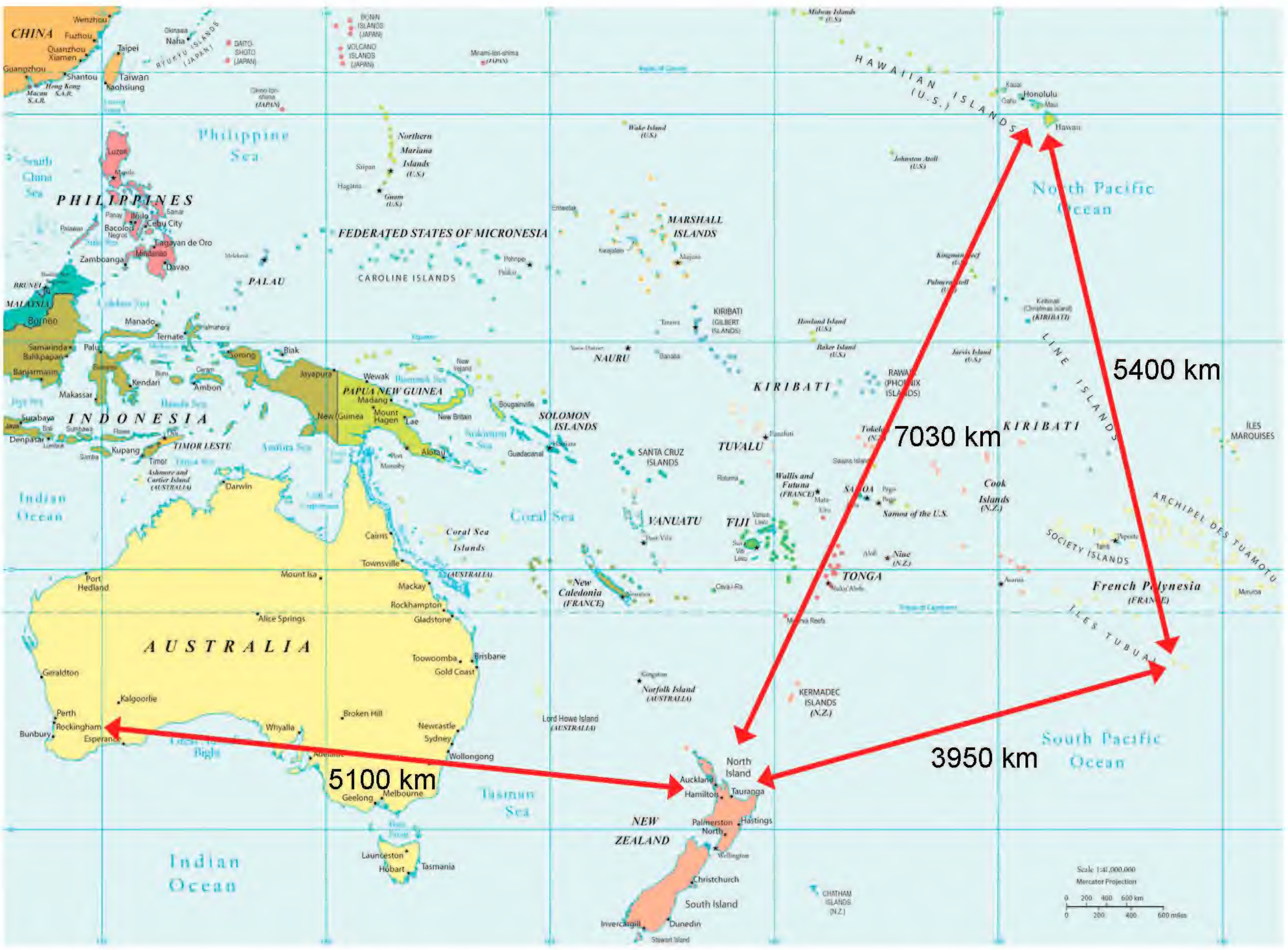

Fig. 1. Location of Rapa Iti and distances between *Morelotia* species in the Pacific Ocean (Hawaii, Rapa Iti and New Zealand) and their nearest relatives in southern Western Australia (adapted by R.L. Barrett from the *CIA World Factbook: Political Oceania*).

Morelotia involuta (H.St John) J.J.Bruhl & R.L.Barrett, *comb. nov*.

Basionym**:** *Machaerina involuta* H.St John, *Nordic J. Bot.* 4: 57, fig. 1 (1984).

Type**:** French Polynesia: Austral Islands, Bass Islands, Rapa Island [Rapa Iti], S of Morongota [Morongo Uta *pare* (fort)], 275 m alt., 8 July 1934, *H. St. John & J. Maireau 15434* (holo: BISH 1001238*; iso: BISH 1001239*, BISH 1001240*, BRI AQ0193095*, GH 00050565*, K!, NSW 1099912!, NY 4106228*, P 00641812*, P 00641813*, SING 0064504*, US 00512838*).

Perennial tufted *herb*, 0.25–0.6 m high; plants clonal, 0.2–0.5 m across; rhizome thick, woody, short, branched, 10–15 mm diam., not pseudobulbous; old leaf sheaths covering the rhizome, breaking apart into fibres and becoming recurved with age, pale brown to dark brown; roots not sand-binding. *Stems* stout, erect, with 1 leafy node above the middle of the culm, trigonous, 1.3–1.7 mm diam., smooth, glabrous, base not or slightly enlarged. *Leaves* mostly basal, numerous, and 1 cauline; phyllotaxy loosely spirotristichous, sheath glabrous, open, 26–38 mm long, 4–5 mm wide, broader than the leaf blade, pale brown, upper margin smooth, ligule absent; basal leaves 20–60 cm long, 2.5–4 mm wide, but involute and appearing 1–1.3 mm wide, lamina ±linear, often twisted or curved, finely multi-striate, glabrous, dark green, paler below, margins very finely scabrous, usually recurved, apex gradually attenuate; cauline leaf blade 15–25 cm long. *Inflorescence* a dense panicle, narrow, linear, 10.5–21 cm long, 5–10 mm diam., with 5–8 fertile nodes; axis green; bracts leaf-like, with pale brown sheaths 15–25 mm long, becoming progressively smaller up the stem, exceeding the spikelet clusters, basal bract longer than inflorescence; branches 20–25 mm long, erect, with (1)2 or 3 clustered spikelets on peduncles 0.5–3 mm long, arising in each bract axil; cladoprophyll subtending each spikelet glume-like, sheath 3.5–4.2 mm long, brown, with 1 distinct vein, partially enclosing the spikelet, with a slender blade 1.8–2.1 mm long, brown. *Spikelets* brown, lanceolate 7–9 mm long, 1.3–1.5 mm diam., ascending, not compressed, with usually 7 glumes, only topmost fertile, bisexual, lower glumes empty, glumes distichous, lowest glume 4 mm long, upper glumes 8–9 mm long, 1.7–2.1 mm wide, glabrous, lanceolate, acuminate, weakly keeled, with a mucro to 3 mm long; rachilla compact and not sinuous in fruiting spikelets. *Perianth segments* present, bristles *c*. 6, inconspicuous, filiform, glabrous, 0.4–1.1 mm long, 1/5–1/3 as long as the nutlet. *Stamens* 3; anther connective 5.1–6.8 mm long, linear, persistent at base of nutlet, distal portion held within the convolute apex of subtending glume, so mature nutlets pendent on the inflorescence post-release; anthers pale yellow, 4–5 mm long, linear-oblong, base auriculate, with a glabrous apical appendage up to 2 mm long. *Style* 3-fid, white; undivided part 3–5 mm long, glabrous, thin throughout; branches 7–10 mm long, hispidulous. *Nutlet* sessile, angular ellipsoid, subterete, but perceptibly 3-sided, mostly stramineous but apex brown and only slightly or not constricted, smooth, 2.1–2.7 mm long including the style base, 0.8–1.0 mm diam., epidermal cells square–hexagonal, but inconspicuous; style base cylindric, hard, persistent, glabrous, *c*. 0.5 mm long and wrinkled when immature, expanding to *c*. 0.7 mm long, smooth and somewhat angular due to continuation of ribs from nutlet. (Figure 2).

Diagnostic characters: Differs from *M. affinis* in: Stems with 1 leafy node (*vs* 0–2(–4) leafy nodes), 1.3–1.7 mm diam. (*vs* 1.9–3.5 mm). Leaf sheath 26–38 mm long (*vs* 35–60 mm). Basal leaves 2.5–4 mm wide (*vs* 4–8 mm), but involute and appearing 1–1.3 mm wide (*vs* 1.5–2.1 mm wide), margins very finely scabrous, (*vs* harshly scabrous), usually recurved (*vs* strongly revolute) when dry. Inflorescence branches 20–25 mm long (*vs* 20–70 mm), with (1)2 or 3 clustered spikelets (*vs* 3–15). Perianth segments present, filiform, 0.4–1.1 mm long (*vs* absent). Nutlet mostly stramineous but apex brown (*vs* lustrous red-brown to black, apex black).

Distribution: Until 2020, only known from seven collections made on one expedition in July 1934 and another in 2002 on Rapa Iti in the Austral Islands, French Polynesia, where it is apparently endemic. Targeted surveys for the species in March 2020 located at least seven populations on Rapa Iti (Figure 3).

Habitat: Grassy volcanic slopes, crests and ridges in open, often disturbed, sunny fernlands with scattered remnant or marginal trees between 80 and 400 m elevation (Figure 4) Recorded in association with *Aristida aspera*, *Asplenium polyodon*, *Athyrium membranaceum*, *Blechnum vulcanicum*, *Bolbitis lonchophora*, *Callistopteris calyculata*, *Coprosma rapensis*, *Cyathea medullaris*, *Cyperus brevifolius*, *Dianella adenanthera*, *Dicranopteris linearis*, *Dryopteris stokesii*, *Elaphoglossum meyeri*, *Eragrostis brownei*, *Erythrina variegata*, *Eurya japonica* var. *nitida*, *Ficinia nodosa*, *Fitchia rapensis*, *Gahnia aspera*, *Glochidion longfieldiae*, *Haloragis stokesii*, *Histiopteris incisa*, *Hymenophyllum* sp., *Lycopodiella cernuua*, *Lycopodiella venustulum*, *Metrosideros collina*, *Peperomia rapensis*, *Pittosporum rapense*, *Rhynchospora stokesii*, *Vaccinium rapense* and *Veronica rapensis* collected in the vicinity. Introduced taxa recorded in direct association include *Bidens pilosa*, *Miscanthus floridulus*, *Pinus caribaea* and *Psidium cattleyanum*.

Fig. 2. *Morelotia involuta*, Rapa Iti, French Polynesia. A, B: Plant habit with mature inflorescences. C: Flowering inflorescence. D: Close-up of inflorescence with fresh styles and old anthers. Photos: R. Taputuarai.

Phenology: Flowers recorded for March and April. Fruit recorded for April and July.

Specimens and images examined: French Polynesia: Austral Islands, Bass Islands, Rapa Iti, E slope of Mt Ruatara, 260 m., 9 July 1934, *F.R. Fosberg 11453* (L*, S*, US*), *loc. cit*., 8 July 1934, *F.R. Fosberg 11454* (P*, US*); sentier vers le Mont Maungaoa, 400 m, 21 Mar. 2002, *J-Y. Meyer 1007 & R. Fenstemacher* (PAP, PTBG 1000028324*); just west of Area village, 80 m, 19 Mar. 2002, *T.J. Motley 2621 & R. Fenstemacher*, collected by *J.-F. Butaud* (PAP, PTBG 1000028319*); Mt. Manguoa (Marugaoa) on ridge just east of Pa (fortress), 380 m, 8 Apr. 2002, *T.J. Motley 2721 & R. Fenstemacher* (PAP, PTBG 1000028323*); Hiri Valley, back slopes below Pukumaru Peak, north facing slope, 400 ft, 13 Apr. 2002, *S. Perlman 18062* (PAP, PTBG 1000028318*); Maunga'ai'ai, sur les flancs du fort, 20 May 2020, *R. Taputuarai 859, 860* (PAP).

Conservation: Remnant native habitats in Rapa Iti are commonly heavily invaded by *Psidium cattleyanum*, *Rubus rosifolius*, *Hedychium flavescens* and weedy grasses, particularly *Melinis minutiflora*, *Miscanthus floridulus* and several *Paspalum* species (Meyer 1996; Mueller-Dombois and Fosberg 1998; Meyer *et al*. 2019), and in some areas by the naturalized Caribbean pine *Pinus caribaea*. This species is likely to be threatened by habitat loss or fragmentation. Fire and goats are additional threats that appear to be increasing (Meyer *et al*. 2014).

It is noted that Brown (1931) did not examine any material of this taxon for his treatment of Cyperaceae in the *Flora of Southeastern Polynesia*, despite collections of other Cyperaceae from nearby locations on Rapa,

Fig. 3. Populations of *Morelotia involuta* on Rapa Iti, French Polynesia located in May 2020. Map by R. Taputuarai.

suggesting the species may have already been quite rare at the time of preceding expeditions, though it may have simply been overlooked given the diversity of 'more interesting' species on the island.

Surveys in 2002 aimed at documenting all vascular plants on the island located four populations, though they were not recognised as *Machaerina involuta* at the time.

Targeted surveys in March 2020 located populations on the Maunga'ai'ai ridge, on the many ridges above Tukou, above Akatamiro Bay, above Anarua Bay, below Vairu (on the Tupuaki side and Haurei Bay side, with most populations occurring between 100 m and 400 m altitude (Figure 4). It was found growing in highly exposed situations in low, open fernlands dominated by *Dicranopteris* and *Lycopodiella*, with some disturbance by feral cattle and goats. At the scale of Rapa Iti as a whole, the species is very sparsely distributed in small populations and as a local endemic, all populations are likely to be subject to the same threats.

Fig. 4. Habitat of *Morelotia involuta* on Rapa Iti, French Polynesia. A, B: Maunga'ai'ai site in fernland with introduced *Psidium cattleyanum* and *Pinus caribaea*. C: Habitat on slopes at Tukou. D: Habitat on ridgelines looking east from Vairu. Photos by R. Taputuarai.

Following the IUCN (2012) threat classification system, we assess *Morelotia involuta* as Endangered (EN). The IUCN alphanumeric summary of our evaluation of criteria and subcriteria is: B1b(iii, iv); B2a; B2b(iii); C1; C2a(i); D2. These criteria are defined as: B1, extent of occurrence less than 20,000 km^2; B1b(iii, iv) continuing decline inferred in area, extent and quality of habitat and number of mature individuals; B2, total area of occupancy less than 2000 km^2; B2a, severely fragmented and known to exist as no more than 10 populations; B2b(iii, v), continuing decline inferred in area, extent and quality of habitat and number of mature individuals; C1, an estimated continued decline of at least 10% within three generations; C2a(i), a projected decline in the number of individuals and no subpopulation estimated to contain more than 1000 mature individuals; D2, populations very restricted area of occupancy, less than 10 km^2 such that it is prone to human activities or stochastic events within a short time period. Threats to *M. involuta* include fire frequency, habitat degradation by feral goats and cattle, competition with non-native plants, particularly *Psidium cattleyanum*, and climate change (mainly increased air temperature).

Etymology: St John (1984) named the species from the Latin *involvo* (I roll in), presumably intending *involvere* (to roll in), in reference to the involute leaf blades.

Notes: St John (1984) allied his *Machaerina involuta* to *M. schoenoides* (R.Br.) Koyama [=*Machaerina acuta* (Labill.) J.Kern], a relationship that is only based on superficial morphological similarities.

Most of the fruit on the isotype at NSW are immature, with small style bases, but a few mature fruit are present on this specimen, with greatly enlarged style bases.

A specimen at US suggests the collection location was on Tubuai Island, but this is an error. St John did collect on Tubuai Island, but three months later than his collections from Rapa Iti, and the Morongo Uta *pare* (fort) is on Rapa Iti. The confusion may have arisen as Rapa Iti is part of the Austral Islands, sometimes referred to as the Tubuai Islands.

Notes on other Cyperaceae from Rapa Iti

Carex rapaensis (H.St.John) K.L.Wilson, *Bot. J. Linn. Soc.* 179: 36 (2015). *Uncinia rapaensis* H.St.John, *Nordic J. Bot.* 4(1): 60 (1984).

Type: French Polynesia, Austral Islands, Rapa, Kamaru, Mt. Perahu, 475 m, 13 July 1934, *H. St. John & J. Maireau 15521* (holo: BISH 1001258*; iso: BISH 1001257*, GH 00050566*, K 000960349*, P 00641823*, US 00512839*).

Sparsely distributed on Rapa Iti, observed along the crest of the summit ridge in cloud forest, along the Munga'ai'ai ridge, below Karere summit in wet forest and on the Parau-Namuere ridge, where it is locally common at each site. (Figure 5).

This species may be the same as the widespread Pacific species *Carex uncinata* L.f. (*Uncinia uncinata* (L.f.) Kük.), with further studies in progress to determine its taxonomic status (K.L. Wilson in prep.).

Carex stokesii F.Br., *Bull. Bernice P. Bishop Mus.* 84: 116, fig. 13 (1931).

Fig. 5. *Carex rapaensis*, Rapa Iti, French Polynesia. A: Plant habit. B, C: Inflorescence. D: Mature infructescence. Photos: R. Taputuarai.

Type: French Polynesia, Austral Islands, Rapa, 100+ m, 21 September 1921, [?*A.M.*] *J.F.G.Stokes 244A* (holo (mounted on two sheets): BISH 1001205*, BISH 1001206*).

=*Carex stokesii* F.Br. var. *aristata* F.Br., F.Br., *Bull. Bernice P. Bishop Mus.* 84: 117 (1931), *syn. nov.*

Type: French Polynesia, Austral Islands, Rapa, 1922, *E.H.Quayle s.n.* (holo: BISH 1001207*; iso: P 00586720*).

Brown (1931) distinguished his variety *aristata* based on the single spikelets (*vs* 1–3) in bract axils and 10-veined perigynium (*vs* 3–5 veined). These characters are both considered to be variable in the species and we do not currently accept the variety as distinct. Common on Rapa Iti, from the seashore to plains and ridges, with some plants extending to the summit of the peaks (Figure 6).

Fig. 6. *Carex stokesii*, Rapa Iti, French Polynesia. A–C: Plant habit. B: Mature infructescence. Photos: A, B: J.-Y. Meyer. C, D: R. Taputuarai.

Carex sp. (*R.Taputuarai 861*)

Just three tussocks of a currently unidentified species with affinity to *Carex uncinata* were found at a single locality along the Kaimuru ridge, below Pakumaru Rock, on the Anarua side. The leaves were paler and broader than those here assigned to *C. rapaensis* and the inflorescence appears to be more compact, but this may simply be variation due to growth conditions. They were growing in a *Metrosideros – Cyathea – Freycinetia* wet

forest that has been invaded by *Psidium cattleyanum*. Detailed morphological studies are yet to be undertaken to determine its taxonomic and therefore conservation status (Figure 7).

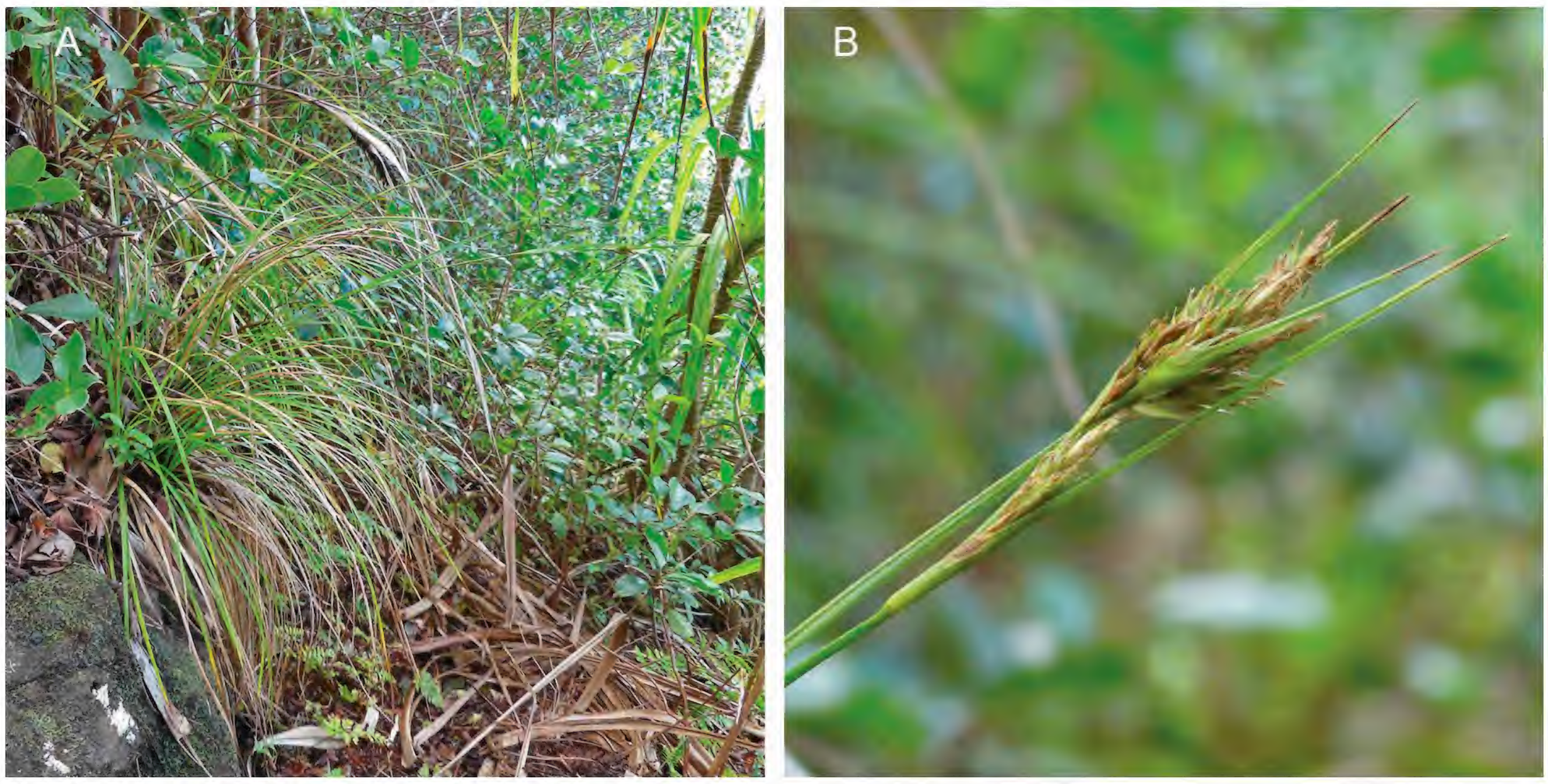

Fig. 7. *Carex* sp., Rapa Iti, French Polynesia. A: Plant habit and habitat. B: Mature inflorescence. Photos: R. Taputuarai.

Cyperus rapensis F.Br., *Bull. Bernice P. Bishop Mus.* 84: 98, pl. X c (1931).

Type: French Polynesia, Austral Islands, Rapa, 1922, *E.H.Quayle 339* (holo: BISH 1001224*; iso: BISH 1001223*).

Poorly known on Rapa Iti, with three collections and one recent observation on open rocky slopes. Also known from Raivavae (Sykes 2016) (Figure 8).

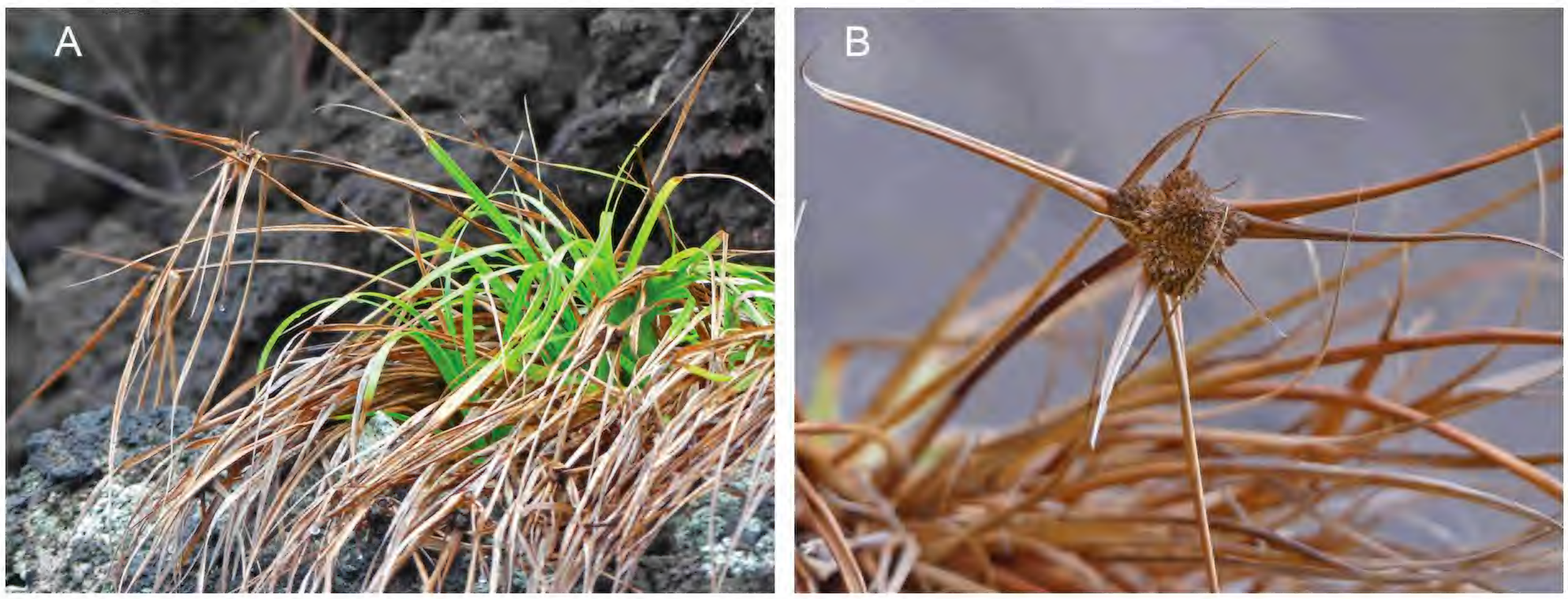

Fig. 8. *Cyperus rapensis*, Rapa Iti, French Polynesia. A: Plant habit. B: Mature infructescence. Photos: R. Taputuarai.

Eleocharis geniculata (L.) Roem. & Schult., *Syst. Veg.* 2: 150 (1817). *Scirpus geniculatus* L., *Sp. Pl.* 1: 48 (1753).

Type: Jamaica: Herb. Clifford 21, Scirpus 1 (lecto: BM 000557653), designated by Furtado, *Gard. Bull. Straits Settlem.* 9: 299 (1937).

=*Eleocharis caribaea* S.F.Blake var. *stokesii* F.Br., *Bull. Bernice P. Bishop Mus.* 84: 106, pl. XIV b (1931).

Type: French Polynesia, Austral Islands, Rapa, 14 September 1921, *J.F.G.Stokes 180* (holo: BISH 1001227*).

Plants described as *Eleocharis caribaea* var. *stokesii* are not considered distinct from the widespread tropical species *E. geniculata*, the type collection merely being a slightly depauperate form. Brown (1931) did not explicitly state why he considered the variety to differ from typical *E. caribaea* (Rottb.) S.F.Blake (=*E. geniculata*) and we can find no clear morphological distinction. In coastal marshes on Rapa Iti.

Gahnia aspera (R.Br.) Spreng., *Syst. Veg.* 2: 114 (1825); *Lamprocarya aspera* R.Br., *Prodr.* 238 (1810); *Cladium asperum* F.Muell., *Fragm.* 9: 12 (1875); *Mariscus asper* (R.Br.) Kuntze, *Revis. Gen. Pl.* 2: 755 (1891), *nom. illeg.*

Type: New South Wales: Port Jackson, 1802, *R.Brown* [*Bennett No. 6061*] (lectotype (here designated): BM000991120; isolecto: BM000991121).

Fig. 9. *Gahnia aspera*, Rapa Iti, French Polynesia. A: Plant habit. B: Mature infructescence. C. Infructescence with mature fruit. Photos: A, B: R. Taputuarai. C: J.-Y. Meyer.

Residual syntypes: Australia: 1770, *J.Banks & D.C.Solander s.n.* (syn: BM000991123, BM000991124); from Port Curtis (Port 1) to Broad Sound, 1802, *R.Brown s.n.* (syn: BM00099119, BM0009922).

=*Gahnia stokesii* F.Br., *Bernice P. Bishop Mus. Bull.* 84: 113, pl. XIV a (1931).

Type: French Polynesia: Austral Islands, Raivavae, Mount Taraia, alt. 274 m, 10 March 1922, *J.F.G.Stokes 38* (holo: BISH 1001234*).

Gahnia stokesii was described as a new species from Raivavae and Rapa Iti, but it clearly belongs to the widespread *G. aspera* complex. Further study is required across the range of *G. aspera* subsp. *aspera s. lat.* before any segregate taxa can be justified and we include *G. stokesii* within *G. aspera* subsp. *aspera*, a taxon which has dispersed widely across the western Pacific from Australia. We consider it common on Rapa Iti, from the seashore, to plains and ridges, with some plants extending to the summit of the peaks (Figure 9).

Rhynchospora stokesii F.Br., *Bull. Bernice P. Bishop Mus.* 84: 109 (1931). *Rhynchospora sclerioides* var. *stokesii* (F.Br.) Kük., *Bot. Jahrb. Syst.* 74: 505 (1949).

Type: French Polynesia, Austral Islands, Rapa, Pariati, between Kapitanga and Kalele, on side of ridge, 280 m alt., 19 October 1921, *J.F.G.Stokes 362* (holo: BISH 1001249*; iso: BISH 1001250*).

=*Rhynchospora stokesii* forma *saxicola* F.Br., *Bull. Bernice P. Bishop Mus.* 84: 110 (1931).

Type: French Polynesia, Austral Islands, Rapa, Nukumaala, on face of cliff, by waterfall, 70 m alt., 21 September 1921, *J.F.G.Stokes 264* (holo: BISH 1001251*; BISH 1001252*).

On slopes in remnant vegetation on Rapa Iti. (Figure 10). Brown (1931) described this as merely a 'dwarf form' and we consider this morphological reduction to be entirely due to the exposed habitat of the type specimen, with no taxonomic significance.

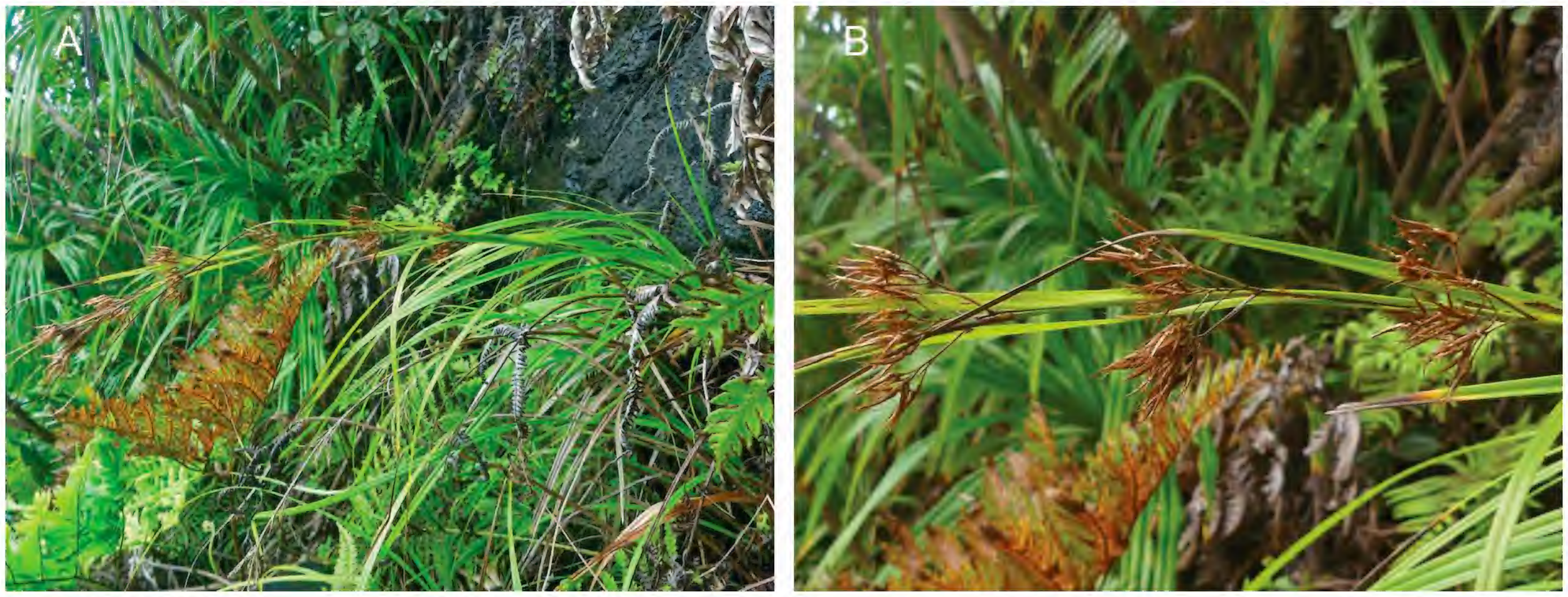

Fig. 10. *Rhynchospora stokesii*, Rapa Iti, French Polynesia. A: Plant habit. B: Mature infructescence. Photos: R. Taputuarai.

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References

Baldwin BG, Wood KR (2016) Origin of the Rapa endemic genus *Apostates*: revisiting major disjunctions and evolutionary conservatism in the *Bahia* alliance (Compositae: Bahieae). *Taxon* 65: 1064–1080. http://dx.doi.org/10.12705/655.8

Barrett RL, Bruhl JJ, Goetghebeur P, Larridon I, Mills KR, Muasya AM, Plunkett GT, Wilson KL (2017) Tribe Schoeneae (Cyperaceae): the taxonomic iceberg of sedges. Pp. 126–126 in *XIX International Botanical Congress: abstract book I: oral presentations*. Shenzhen, China)

Barrett RL, Bruhl JJ, Wilson KL (2021) Revision of generic concepts in Schoeneae subtribe Tricostulariinae (Cyperaceae) with a new Australian genus *Ammothryon* and new species of *Tricostularia*. *Telopea* 24: 61–169. https://doi.org/10.7751/telopea14454

Barrett RL, Wilson KL, Bruhl JJ (2019) *Anthelepis*, a new genus for four mainly tropical species of Cyperaceae from Australia, New Caledonia and South East Asia. *Australian Systematic Botany* 32: 269–289. https://doi.org/10.1071/SB18047

Barrett RL, Wilson KL, Bruhl JJ (2020) Reinstatement and revision of the genus *Chaetospora* (Cyperaceae: Schoeneae). *Telopea* 23: 95–112. https://doi.org/10.7751/telopea14345

Benl G (1940a) Die systematik der gattung *Gahnia* Forst. *Botanisches Archiv* 40: 151–257.

Benl G (1940b) Nomina nova vel emendata generis *Gahniae* Forst. *Feddes Repertorium* 49: 30–34.

Benl G (1950) Zur systematik der Cyperaceengattung *Gahnia* Forst. *Botanische Jahrbucher* 75: 82–89.

Blake ST (1969) Studies in Cyperaceae. *Contributions of the Queensland Herbarium* 8: 1–48.

Brown FBH (1931) *Flora of Southeastern Polynesia. I, Monocotyledons. Bernice P. Bishop Museum Bulletin 84.* (The Museum: Honolulu, Hawaii)

Bruhl JJ (1995) Sedge genera of the world: relationships and a new classification of the Cyperaceae. *Australian Systematic Botany* 8: 125–305. https://doi.org/10.1071/SB9950125

Bruhl JJ, Barrett RL, Barrett MD, Hodgon J, Verboom AG, Muasya AM, Henning JL, Simpson DA, Wilson KL, Morden C, Csiba L, Forest F, Chase MW (2008a) Testing monophyly within Schoeneae - a storehouse of phylogenetic diversity in Cyperaceae. Pp. 100 in *Monocots IV, Abstracts*. (Natural History Museum of Denmark: Copenhagen)

Bruhl JJ, Barrett RL, Barrett MD, Hodgon J, Csiba L, Verboom GA, Muasya AM, Henning JL, Simpson DA, Wilson KL, Morden C, Forest F, Chase MW (2008b) Phylogenetic relationships of Schoeneae (Cyperaceae): the end of the beginning [Abstract]. In: *Australian Systematic Botany Society 2008 National Conference Adelaide. Systematics in a changing environment*. (The University of Adelaide: Adelaide).

Bryson CT, Carter R (1998) The significance of Cyperaceae as weeds. In: Naczi RFC, Ford, BA (eds) Sedges: uses, diversity, and systematics of the Cyperaceae. *Monographs in Systematic Botany from the Missouri Botanical Garden* Vol. 108. pp. 15–101. (Missouri Botanical Garden: St. Louis)

Cain ML, Milligan BG, Strand AE (2000) Long-distance dispersal in plant populations. *American Journal of Botany* 87: 1217–1227.

Chevillotte H, Florence J, Ollier C, Meyer J-Y (2019) Base de données botaniques Nadeaud de l'Herbier de la Polynésie française (PAP). Institut Louis Malardé, Délégation à la Recherche, Papeete, Tahiti. http://nadeaud.ilm.pf [accessed 2 Sept. 2020]

Copeland EB (1948) The origin of the native flora of Polynesia. *Pacific Science* 2: 293–296.

DiNapoli RJ, Morrison AE, Lipo CP, Hunt TL, Lane BG (2018) East Polynesian islands as models of cultural divergence: the case of Rapa Nui and Rapa Iti. *The Journal of Island and Coastal Archaeology* 13: 206–223. http://dx.doi.org/10.1080/15564894.2016.1276490

Florence J (1997) *Flore de la Polynésie française.Volume 1*. Collection faune et Flore tropicales 34. (Editions de l'Orstom: Paris)

Funk VA, Wood K (2014) *Bidens meyeri* (Asteraceae, Coreopsideae): a new critically endangered species from Rapa, Austral Islands. *PhytoKeys* 42: 39–47. https://doi.org/10.3897/phytokeys.42.8408

Garnock-Jones PJ (1976) *Hebe rapensis* (F. Brown) Garnock-Jones comb. nov. and its relationships. *New Zealand Journal of Botany* 14: 79–83. https://doi.org/10.1080/0028825X.1976.10428654

Garnock-Jones P, Albach D, Briggs BG (2007) Botanical names in Southern Hemisphere *Veronica* (Plantaginaceae): sect. *Detzneria*, sect. *Hebe*, and sect. *Labiatoides*. *Taxon* 56: 571–582. https://doi.org/10.1002/tax.562028

Gibbons KL (2020) *Hedyotis*, *Oldenlandia* and related genera (Rubiaceae: Spermacoceae) in Australia: New genera and new combinations in an Asian-Australian-Pacific lineage. *Taxon* 69: 515–542. https://doi.org/10.1002/tax.12236

Gibbons KL, Henwood MJ, Conn BJ (2012) Phylogenetic relationships in Loganieae (Loganiaceae) inferred from nuclear ribosomal and chloroplast DNA sequence data. *Australian Systematic Botany* 25: 331–340. https://doi.org/10.1071/SB12002

IUCN (2012) *IUCN Red List Categories and Criteria: Version 3.1. Second edn. IUCN Species Survival Commission*. (IUCN: Gland, Switzerland and Cambridge, UK)

Iwanycki Ahlstrand N, Verstraete, B, Hassemer G, Dunbar-Co S, Hoggard R, Meudt HM, Rønsted, N (2019) Ancestral range reconstruction of remote oceanic island species of *Plantago* (Plantaginaceae) reveals differing scales and modes of dispersal. *Journal of Biogeography* 46: 706–722. https://doi.org/10.1111/jbi.13525

Jacobs SWL, Wilson KL (1996) A biogeographical analysis of the freshwater plants of Australasia. *Australian Systematic Botany* 9: 169–183. https://doi.org/10.1071/SB9960169

Kern JH (1962) On the delimitation of the genus *Gahnia* (Cyperaceae). *Acta Botanica Neerlandica* 11: 216–224.

Kuijt J, Hansen B (2015) Santalaceae. In: Kubitzki K (ed.) *The Families and Genera of Vascular Plants. Volume 12. Flowering Plants. Eudicots. Santalales, Balanophorales*. pp. 143–166. (Springer International Publishing; Switzerland) https://doi.org/10.1007/978-3-319-09296-6

Kreft H, Jetz W, Mutke J (2008) Global diversity of island floras from a macroecological perspective. *Ecology Letters* 11: 116–127.

Lander NS (1989) *Apostates* (Asteraceae: Astereae), a new genus from the south-eastern Polynesian island of Rapa. *Australian Systematic Botany* 2: 129–133. http://dx.doi.org/10.1071/SB9890129

Larridon I, Bauters K, Semmouri I, Viljoen J-A, Prychid CJ, Muasya AM, Bruhl JJ, Wilson KL, Senterrehi B, Goetghebeur PA (2018a) Molecular phylogenetics of the genus *Costularia* (Schoeneae, Cyperaceae) reveals multiple distinct evolutionary lineages. *Molecular Phylogenetics and Evolution* 126: 196–209. https://doi.org/10.1016/j.ympev.2018.04.016

Larridon I, Verboom GA, Muasya AM (2018b) Revised delimitation of the genus *Tetraria*, nom. cons. prop. (Cyperaceae, tribe Schoeneae, *Tricostularia* clade). *South African Journal of Botany* 118: 18–22. https://doi.org/10.1016/j.sajb.2018.06.007

Larridon I, Rabarivola L, Xanthos M, Muasya AM (2019) Revision of the Afro-Madagascan genus *Costularia* (Schoeneae, Cyperaceae): infrageneric relationships and species delimitation. *PeerJ* 7: e6528. https://doi.org/10.7717/peerj.6528

Meyer J-Y (1996) Tahiti's native flora endangered by the invasion of *Miconia calvescens* DC. (Melastomataceae). *Journal of Biogeography* 23: 775–781.

Meyer J-YH (2002) *Rapport de mission d'exploration botanique à Tubuai et Rapa (Australes) du 13 mars au 5 avril 2002*. (Délégation à la Recherche: Papeete, Tahiti) https://www.li-an.fr/jyves/Meyer_2002_Rapport_mission_Tubuai_&_Rapa.pdf

Meyer J-Y (2004) Threat of invasive alien plants to native flora and forest vegetation of Eastern Polynesia. *Pacific Science* 58: 357–375.

Meyer J-Y (2011) *Rapa, îles Australes. Guide de la flore indigène et endémique*. (Direction de l'Environment, Délégation à la Recherche: Papeete, Tahiti) https://www.service-public.pf/diren/wp-content/uploads/sites/17/2019/01/Rapa.pdf

Meyer J-Y (2014) The Austral islands in French Polynesia. Pp. 13–18 in J-Y Meyer and EM Claridge (Eds) *Terrestrial biodiversity of the Austral Islands, French Polynesia*. Patrimoines Naturels (Book 72). (Muséum National d'Histoire Naturelle: Paris)

Meyer J-Y, Chevillote, H, Motley TJ (2014) Vascular flora, general traits and main threats. In: Meyer J-Y, Claridge EM (Eds) *Terrestrial biodiversity of the Austral Islands, French Polynesia*. pp. 117–132. Patrimoines Naturels (Book 72) (Muséum National d'Histoire Naturelle: Paris)

Meyer J-Y, Claridge EM (2014a) (Eds) *Terrestrial biodiversity of the Austral Islands, French Polynesia*. Patrimoines Naturels (Book 72) (Muséum National d'Histoire Naturelle: Paris)

Meyer J-Y, Claridge EM (2014b) Introduction: multidisciplinary scientific expeditions to assess the terrestrial biodiversity of the Austral Islands. Pp. 7–12 in J-Y Meyer and EM Claridge (Eds) *Terrestrial biodiversity of the Austral Islands, French Polynesia*. Patrimoines Naturels (Book 72). (Muséum National d'Histoire Naturelle: Paris)

Meyer J-Y, Laitame T, Gaertner J-C (2019) Short term recovery of native vegetation and threatened species after restoration of a remnant forest in a small oceanic island of the South Pacific. *Plant Ecology and Diversity* 12: 75–85. https://doi.org/10.1080/17550874.2019.1584651

Moser D, Lenzner B, Weigelt P, Dawson W, Kreft H, Pergl J, Pyšek P, van Kleunen M, Winter M, Capinha C, Cassey P, Dullinger S, Economo EP, García-Díaz P, Guénard B, Hofhansl F, Mang T, Seebens H, Essl F (2018) Remoteness promotes biological invasions on islands worldwide. *Proceedings of the National Academy of Sciences of the United States of America* 115: 9270–9275. www.pnas.org/cgi/doi/10.1073/pnas.1804179115

Motley TJ, Luongo A, Meyer J-Y (2014) Vegetation types and map of Rapa. Pp. 133–148 in J-Y Meyer and EM Claridge (Eds) *Terrestrial biodiversity of the Austral Islands, French Polynesia. Patrimonines Naturels (Book 72)*. (Muséum National d'Histoire Naturelle: Paris)

Muasya AM (2016) The changing generic concepts in Cyperaceae — Cosmopolitan mega-genera and polyphyly of southern African taxa. *South African Journal of Botany* 103: 337. https://doi.org/10.1016/j.sajb.2016.02.125

Mueller-Dombois D, Fosberg FR (1998) *Vegetation of the Tropical Pacific Islands*. (Springer-Verlag: New York)

Musili PM, Gibbs AK, Wilson KL, Bruhl JJ (2017) *Schoenus* (Cyperaceae) is not monophyletic based on ITS nrDNA sequence data. *Australian Systematic Botany* 29: 265–283. https://doi.org/10.1071/SB15046

Neupane S, Dessein S, Wikstrom N, Lewis PO, Long C, Bremer B, Motley TJ (2015) The *Hedyotis-Oldenlandia* complex (Rubiaceae: Spermacoceae) in Asia and the Pacific: Phylogeny revisited with new generic delimitations. *Taxon* 64: 299–322. https://doi.org/10.12705/642.8

Pillon Y, Stacy E, Meyer J-Y (2018) Phylogenetics and systematics of the South Polynesian genera *Apetahia* and *Sclerotheca* (Campanulaceae subfam. Lobelioideae). *Botany Letters* 165: 186–192. https://doi.org/10.1080/23818107.2018.1452792

Prebble M, Anderson A (2012) The archaeobotany of Rapan rockshelter deposits. In *Taking the high ground: the archaeology of Rapa, a fortified island in remote East Polynesia*. A Anderson and DJ Kennett (Eds). pp. 77–95. (ANU E Press: Canberra)

Price JP, Wagner WL (2018) Origins of the Hawaiian flora: phylogenies and biogeography reveal patterns of long-distance dispersal. *Journal of Systematics and Evolution* 56: 600–620. https://doi.org/10.1111/jse.12465

Rouhan G, Dubuisson J-Y, Rakotondrainibe F, Motley TJ, Mickel JT, Labat J-N, Moran RC (2004) Molecular phylogeny of the fern genus *Elaphoglossum* (Elaphoglossaceae) based on chloroplast non-coding DNA sequences: contributions of species from the Indian Ocean area. Molecular Phylogenetics and Evolution 33: 745–763. https://doi.org/10.1016/j.ympev.2004.08.006

Rouhan G, Lorence DH, Motley TJ, Garrison Hanks J, Moran RC (2008) Systematic revision of *Elaphoglossum* (Dryopteridaceae) in French Polynesia, with description of three new species. *Botanical Journal of the Linnean Society* 158: 309–331. https://doi.org/10.1111/j.1095-8339.2008.00858.x

Semmouri I, Bauters K, Léveillé-Bourret É, Starr JR, Goetghebeur P, Larridon I (2019) Phylogeny and systematics of Cyperaceae, the evolution and importance of embryo morphology. *The Botanical Review* 85: 1–39. https://doi.org/10.1007/s12229-018-9202-0

Smedmark JEE, Anderberg AA (2007) Boreotropical migration explains hybridization between geographically distant lineages in the pantropical clade Sideroxyleae (Sapotaceae). *American Journal of Botany* 94: 1491–1505. https://doi.org/10.3732/ajb.94.9.1491

Sorensen AE (1986) Seed dispersal by adhesion. *Annual Review of Ecology and Systematics* 17: 443–463. https://doi.org/10.1146/annurev.es.17.110186.002303

St John H (1958) The status of "*Gahnia affinis*" and "*G. gahniaeformis*" (Cyperaceae) of Polynesia. Pacific plant studies 16. *Webbia* 13: 331–342. https://doi.org/10.1080/00837792.1958.10669679

St John H (1984) *Machaerina* and *Uncinia* (Cyperaceae) on Rapa, Austral Islands. – Pacific plant studies 41. *Nordic Journal of Botany* 4: 57–60. https://doi.org/10.1111/j.1756-1051.1984.tb01972.x

Sykes WR (2016) *Flora of the Cook Islands*. (National Tropical Botanical Garden: Kaua'i, Hawai'i)

van Balgooy MMJ (1971) Plant-geography of the Pacific: as based on a census of phanerogam genera. *Blumea* Supplement 6. (Rijksherbarium: Leyden)

van Balgooy MMJ, Hovenkamp PH, van Welzen PC (1996) Phytogeography of the Pacific – floristic and historical distribution patterns in plants. Pp. 191–213 in Eds A Keast and SE Miller (Ed.) *The origin and evolution of Pacific island biotas, New Guinea to Eastern Polynesia: Patterns and processes*. (SPB Academic Publishing: Amsterdam)

Viljoen J-A, Muasya AM, Barrett RL, Bruhl JJ, Gibbs AK, Slingsby JA, Wilson KL, Verboom AG (2013) Radiation and repeated transoceanic dispersal of Schoeneae (Cyperaceae) through the Southern Hemisphere. *American Journal of Botany* 100: 2494–2508. https://doi.org/10.3732/ajb.1300105

Zhang X, Marchant A, Wilson KL, Bruhl JJ (2004) Phylogenetic relationships of *Carpha* and its relatives (Schoeneae, Cyperaceae) inferred from chloroplast *trn*L intron and *trn*L—*trn*F integenic spacer sequences. *Molecular Phylogenetics and Evolution* 31: 647–657. https://doi.org/10.1016/j.ympev.2003.09.004

Zhang X, Bruhl JJ, Wilson KL, Marchant AD (2007) Phylogeny of *Carpha* and related genera (Schoeneae, Cyperaceae) inferred from morphological and molecular data. *Australian Systematic Botany* 20: 93–106.

Zicus S (2020) *Islands of the South Pacific east of Australia*. https://www.worldwildlife.org/ecoregions/oc0116 [accessed 12 July 2020]. (World Wildlife Fund)

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Contribution to the bryoflora of Australia, V. *Radula tonitrua* sp. nov. from Queensland

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Abstract

Study of two recognised geographic lineages within *Radula novae-hollandiae sens. lat.* have resulted in the detection of morphological differences between individuals from the Queensland Wet Tropics, and those from New South Wales. Individuals from the Wet Tropics have perianths that are shorter at maturity (1.6–2.0 *v.* 3.8–4.4 mm), leaf lobes that usually bear numerous marginal gemmae, and leaf-lobules that are smaller and more quadrate. The morphological differences, particularly in perianth length, were not fully appreciated previously and provide evidence supporting the recognition of the Queensland Wet Tropics lineage as a distinct and new species, *Radula tonitrua*, which is here described. The degree of phylogenetic divergence and fixed molecular difference between *R. tonitrua* and *R. novae-hollandiae*, are comparable with the separation observed between *R. ocellata* and *R. pulchella*, another species pair exhibiting the same geographic disjunction.

Introduction

Paluma Range in Queensland is an isolated, large, rainforest island, surrounded by much drier areas. It is most notable for the northerly occurrence of several otherwise southern rainforest species, and for being a southern limit for many otherwise northern species. At the same time the Paluma Range is the type locality for several recently-described bryophyte taxa, including *Jubula hutchinsiae* ssp. *australiensis* Pócs and Cairns (2008) and *Cololejeunea cairnsiana* Pócs. There are other rare species too, originally reported for Australia based on collections from the Paluma Range, including *Cheilolejeunea ventricosa* (Schiffn.) X.L.He (Pócs and Streimann 2006) and *Nowellia langii* Pears. (Pócs *et al.* 2012). It is likely there are more novelties there to be discovered. During fieldwork collecting material for a revision of the genus *Frullania* in Australia, the first author collected, among other epiphyllous material, a tiny *Radula* species on the leaves of the filmy fern *Abrodictyum obscurum* (Blume) Ebihara & K.Iwats. in the notophyll vine forest of Birthday Creek in Paluma Range of Queensland, near Paluma settlement, at 850 m elevation. The plants bore acute leaves, and two pairs of female bracts, so belonged to subgenus *Odontoradula* K.Yamada. They were similar both to *Radula kojana* Steph. in their copious marginal gemmae and to *Radula novae-hollandiae* Hampe in their leaf and perianth shape. After careful examination it became clear that the specimen does not belong to *R. novae-hollandiae* and proved to be new to science, as both of the above species have much longer perianth (c. 4 mm long), while in the new species the mature perianth hardly exceeds 2 mm length. *Radula novae-hollandiae* infrequently produces gemmae, which are very abundant in the new species. Both known species have narrower stem medulla cells 8–12 μm diameter (in 5–12 or 19–27 rows respectively) while the stem medulla cells of the new

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species are 10–20 μm diameter (in 6 rows). Its stem cortical cells are even larger, some to 30 μm diameter. Otherwise, the shape of sterile and perichaetial leaves (apart from the gemmae) are similar in all three species.

The relationships of 9 Australian species of *Radula* subgenus *Odontoradula* (Yamada 1979) were resolved using chloroplast DNA markers (Renner *et al.* 2013a, 2013b). In their revision of Australian *Radula* (Renner *et al.* 2013a), *Radula novae-hollandiae* was broadly circumscribed, and considered widespread in Australia, including Norfolk Islands, and occurring in New Zealand only in the Kermadec Islands. Two geographic lineages were resolved within *R. novae-hollandiae*, one in south-east Australia, the other in the Wet Tropics Bioregion of north-east Queensland. In this paper we reanalyse the molecular data from Renner *et al.* (2013a), which included *Radula novae-hollandiae s. lat.*, as part of our re-assessment of the plants from the Wet Tropics Bioregion of north-east Queensland, and separate these populations from *R. novae-hollandiae* as a new species.

Materials and Methods

Taxon sampling and molecular protocols

Sampling for DNA was based on material collected haphazardly throughout the Australasian geographical ranges reported for species of *Radula* subg. *Odontoradula*. This includes the Wet Tropics bioregion in north-eastern Queensland, along the coast and Great Dividing Range through New South Wales, Victoria, Tasmania and in New Zealand, for the purposes of the revision of *Radula* subg. *Odontoradula* published by Renner *et al.* (2013a). The objective of collecting was to sample individuals of each species from many sites across their range. Clean shoot tips comprising the meristem, embryonic leaves, and one or two nearly mature leaves were excised from each specimen until ~25–50 mm^2 of cleaned material was obtained, depending on plant size. DNA samples were either stored on silica gel or rapidly air-dried from wild-collected material to ensure plant material remained green and fungus-free.

Total genomic DNA was extracted using the DNeasy Plant Minikit (QIAGEN, Sydney, Australia), and three chloroplast markers were sequenced: (1) the *atpB–rbcL* spacer; (2) the plastid *trnL–F* region including the trnLUAA group1 intron and the *trnL–F* intergenic spacer, hereafter *trnL–F*; and (3) the *trnG* G2 intron. These regions were chosen because universal primers are available for all; they are known to exhibit sufficient variation to be informative at a species level (Stech and Quandt 2010) and two were used by Devos *et al.* (2011a, 2011b) to reconstruct the phylogeny of *Radula,* meaning a broader phylogenetic sampling context for the investigation of *R. novae-hollandiae* is available. Primer details were provided in Renner *et al.* (2013a). Polymerase chain reaction (PCR) was carried out as follows, for *trnL–F*, each 15-mL reaction contained 1.5 mL of 10′ PCR Buffer, 1.5 mL of 20 mM $MgCl_2$, 0.9 mL of each primer at 10-mM concentration, 0.12 mL of 1% BSA, and 0.12 mL of Immolase Taq (Bioline, Sydney, NSW). For the *atpB–rbcL* and *trnG*, each 15-mL reaction contained 1.5 mL of 10′ PCR buffer, 0.75 mL of 20 mM $MgCl_2$, 0.9 mL of each primer at 10-mM concentration, 0.12 mL of 1% BSA and 0.08 mL of Immolase Taq. Temperature profiles used for sequencing of *trnL–F* and *trnG* were 95°C for 10 min, then 35 cycles of 95°C for 1 min, 1 min at annealing temperature of 53°C, then 72°C for 1 min, followed by a final extension step of 72°C for 10 mins. The same profile, but with an annealing temperature of 50°C was used for atpB–rbcL. Cleaned PCR products were sequenced by Macrogen, South Korea (www.macrogen.com, accessed 24 February 2014) using the same primers as in PCR reactions.

Sequences were assembled using Geneious v.6 (Drummond *et al.* 2012), and consensus sequences were aligned by MUSCLE (Edgar 2004) on the CIPRES portal (Miller *et al.* 2010) and manually edited in BioEdit 5.0.9 (Hall 1999). jModelTest 2.1.10 (Darriba *et al.* 2012) to select optimal substitution models for each partition, from among 56 candidate models, with the corrected Akaike Information Criterion as the measure of model fit on the ML optimized tree. For the *atpB-rbcL* spacer an unequal frequency TVM+G model was selected as optimal, we used the next best model, which was GTR+G. For *trnG* an unequal frequency TPM1+I+G was selected as optimal, we used the next best fitting model, which was HKY+I+G; and for *trnL–F* an unequal frequency TPM1+G was selected as optimal, we used the next best fitting model but one, which was HKY+G, as this was easily implemented in BEAST.

We reconstructed relationships under maximum likelihood with iQTree (Nguyen *et al.* 2015), with a partitioned model (Cernomor *et al.* 2016) with a separate substitution model for each molecular marker, with the substitution models identified following model selection. We used the ultrafast bootstrapping approximation (Mihn *et al.* 2013; Hoang *et al.* 2018) as a measure of support for each branch. We estimated ultrametric trees summarising relationships using BEAST v.1.4.8 (Drummond and Rambaut 2007). Base frequencies were estimated, and six gamma categories were assigned for each substitution model, with all substitution models and clock models unlinked, but trees for the three partitions were linked. Substitution model priors followed default settings in BEAUTi v.1.7.2 (Drummond and Rambaut 2007). A separate uncorrelated log-normal relaxed clock modelled

substitution rates for each partition, with rates estimated relative to *atpB–rbcL*. A uniform prior with a range of 0–100 was applied to each clock, a speciation birth–death model (Gernhard 2008) with a uniform distribution was applied to node heights, and an unweighted pair-group mean aggregate (UPGMA) dendrogram was used as the starting tree. The phylogeny was not time-calibrated, however the branches in resulting ultrametric trees are proportional to time. The analysis was replicated three times, each was run for 20 million generations and sampled every 1000. Burn-in length and convergence were confirmed by comparing trace files in Tracer v.1.5 (Rambaut and Drummond 2009). After excluding the first 10% of samples as burn-in, the maximum clade credibility tree summarised the sample of trees from the posterior probability distribution.

Automatic barcode gap discovery (ABGD)

Automatic barcode gap discovery (ABGD) distinguishes distances resulting from coalescence from those resulting from divergence, by identifying the first significant peak in a plot of ranked pairwise genetic distances, which is interpreted as the gap separating intra- from inter-specific difference (Puillandre *et al.* 2012; Fontaneto *et al.* 2015). ABGD was applied to the concatenated chloroplast markers through the ABGD web portal (http://www.abi.snv.jussieu.fr/public/abgd/, accessed 16 November 2020), with default settings and distance matrices calculated using K80.

Generalised mixed Yule coalescent (GMYC) analysis

Generalised mixed Yule coalescent (GMYC) analysis (Pons *et al.* 2006) uses the expectation that coalescent branching within species occurs more rapidly than do speciation events between species. Therefore, species in gene trees form clusters of individuals on short branches separated from other such clusters by longer internal branches. Because they share the same gene tree by virtue of inheritance in plastid DNA, the concatenated chloroplast markers were used for estimation of an ultrametric gene tree. Single and multiple threshold model GMYC analyses were performed in R, ver. 3.5.2 (R Foundation for Statistical Computing) with the splits (see http://R-Forge.R-project.org/projects/splits/, accessed 16 November 2020) and ape (Paradis *et al.* 2004) packages, based on the ingroup, comprising subg. *Odontoradula*, only.

Fixed differences

Groups based on molecular data and morphological characters were compared in DnaSP v.5 (Librado and Rozas 2009). For each group, only individuals for which all three markers were sequenced were included.

Results

Voucher data and associated GenBank numbers for the molecular markers analysed for the ingroup samples belonging to *Radula* subg. *Odontoradula* are given in Table 1. *Radula novae-hollandiae* was resolved monophyletic with full support, in a sister relationship with *R. acuta*, a relationship that received support as measured by ultrafast bootstrap, but had low posterior probability. The *R. novae-hollandiae* plus *R. acuta* monophylum was in turn sister to a strongly supported clade containing *R. kojana*, and *R. apiculata* (Fig. 1). This clade was sister to *R. cuspidata*, and in turn in a fully supported sister relationship to *R. pulchella* plus *R. ocellata*. Parameter traces confirmed stationarity and convergence of all three runs, with effective sample sizes for tree likelihood and substitution model parameters greater than 200 in all three. Relationships resolved in maximum likelihood and Bayesian trees differed in the relationships close to the base of the tree, with *R. decora* plus *R. tasmanica* forming an unsupported monophylum sister to the remainder of the subgenus in the maximum likelihood tree, whereas in the Bayesian MCC tree *R. decora* plus *R. tasmanica* formed a monophylum with *R. plicata*, which was sister to the lineage containing *R. pulchella* and others, but without support. *Radula novae-hollandiae* was subdivided into two fully supported clades, one comprising individuals from north-east Queensland the other individuals from south-eastern Australia.

Automatic barcode gap discovery (ABGD)

ABGD results were in broad agreement, but exhibited some variation in grouping on the minimal prior inter-specific distance and the distance metric. *Radula ocellata* and *R. pulchella* were both oversplit under JC and K80 distances. While the north-east Queensland and south-east Australian lineages of *R. novae-hollandiae* were delimited as different clusters under JC and K80 distances metrics, under simple distance they were grouped together in a single cluster. All *Radula tasmanica* were grouped in a single cluster on JC and K80 distances, but were divided on geography into two clusters on the simple distance metric.

Table 1: Voucher specimens and associated GenBank numbers for sequences from three molecular markers analysed in this study, for ingroup accessions belonging to *Radula* subg. *Odontoradula*.

Species	Country	Region	Collector	number	Collection date	Voucher	atpB-rbcL	trnG	trnLF
R. acuta	Fiji	Viti Levu	M.A.M. Renner	5330	29 August 2011	NSW889318	KF495328	KF495267	KF495387
R. acuta	Fiji	Viti Levu	M.A.M. Renner	5349	29 August 2011	NSW889366	KF495330	KF495268	KF495389
R. acuta	Fiji	Viti Levu	M.A.M. Renner	5416	31 August 2011	NSW889521	KF495331	KF495269	KF495390
R. acuta	Fiji	Viti Levu	M.A.M. Renner	5503	1 September 2011	NSW890194	KF495334	KF495272	KF495393
R. acuta	Vanuatu	Sanma	E.A. Brown	s.n.	November 2006	NSW971056	KF495361	KF495302	KF495418
R. acuta	Fiji	Viti Levu	M.A.M. Renner	5346	29 August 2011	NSW889362	KF495329	–	KF495388
R. allisonii	New Zealand	North Island	M.A.M. Renner	6264	24 February 2012	NSW896403	KF495342	KF495280	KF495397
R. allisonii	New Zealand	North Island	M.A.M. Renner	6269	24 February 2012	NSW896414	KF495343	KF495281	KF495398
R. allisonii	New Zealand	North Island	P.J. de Lange	10144	22 September 2011	NSW973432	KF495367	KF495307	KF495423
R. allisonii	New Zealand	North Island	P.J. de Lange	s.n.	22 September 2011	NSW973436	KF495368	KF495308	KF495424
R. allisonii	New Zealand	South Island	M.A.M. Renner	6072	12 February 2012	NSW895347	KF495337	KF495275	KF495395
R. apiculata			T. Yamaguchi	1731		BR	HM992050	-	HM992478
R. cuspidata	New Zealand		M.A.M. Renner			AK280588	HM992002	HM992353	HM992439
R. decora			I. Holz & Franzaring	CH0060		GOET	HM991973	HM992327	HM992413
R. kojana	Japan		M. Mizutani	14255		DUKE	HM992013	HM992364	HM992447
R. novae-hollandiae	Australia	NSW	M.A.M. Renner	5261	14 April 2011	NSW875807	KF495322	KF495261	KF495381
R. novae-hollandiae	Australia	NSW	M.A.M. Renner	5274	15 April 2011	NSW875820	KF495323	KF495262	KF495382
R. novae-hollandiae	Australia	NSW	M.A.M. Renner	5883	16 December 2011	NSW898670	KF495354	KF495293	KF495410
R. novae-hollandiae	Australia	NSW	M.A.M. Renner	5024	22 September 2010	NSW973484	KF495369	KF495309	KF495425
R. novae-hollandiae	Australia	NSW	M.A.M. Renner	5036	22 September 2010	NSW973485	KF495370	KF495310	KF495426
R. novae-hollandiae	Australia	Qld	M.A.M. Renner	2110	13 July 2005	NSW885020	KF495327	KF495266	KF495386
R. novae-hollandiae	Australia	Qld	M.A.M. Renner	6341	27 March 2012	NSW896746	KF495347	KF495285	KF495402
R. novae-hollandiae	Australia	Qld	M.A.M. Renner	6362	28 March 2012	NSW896816	KF495348	KF495286	KF495403
R. novae-hollandiae	Australia	Qld	M.A.M. Renner	6366	27 March 2012	NSW896820	KF495349	KF495287	KF495404
R. novae-hollandiae	Australia	Qld	M.A.M. Renner	6401	30 March 2012	NSW896902	KF495350	KF495288	KF495405
R. novae-hollandiae	Australia	Qld	M.A.M. Renner	6436	30 March 2012	NSW896975	KF495351	KF495289	KF495406
R. novae-hollandiae	Australia	Qld	M.A.M. Renner	6443	30 March 2012	NSW896982	KF495352	KF495290	KF495407
R. novae-hollandiae	Australia	Qld	M.A.M. Renner	6514	5 April 2012	NSW898725	KF495356	KF495295	KF495412
R. novae-hollandiae	Australia	Qld	M.A.M. Renner	6547	5 April 2012	NSW973523	KF495371	KF495311	KF495427
R. ocellata	Australia	Qld	M.A.M. Renner	5093	26 January 2011	NSW970362	–	KF495299	KF495415
R. ocellata	Australia	Qld	M.A.M. Renner	5090	26 January 2011	NSW970874	KF495360	KF495301	KF495417
R. ocellata	Australia	Qld	M.A.M. Renner	5091	26 January 2011	NSW973669	KF495372	KF495312	KF495428
R. ocellata	Australia	Qld	M.A.M. Renner	5108	28 January 2011	NSW973771	KF495373	KF495313	KF495429
R. ocellata	Australia	Qld	M.A.M. Renner	5053	24 July 2011	NSW973946	KF495374	KF495314	KF495430
R. ocellata	Australia	Qld	M.A.M. Renner	5054	24 July 2011	NSW973994	–	KF495315	KF495431
R. ocellata	Australia	Qld	J.A. Curnow	3664		CBG	HM992003	HM992354	HM992440

Species	Country	Region	Collector	number	Collection date	Voucher	atpB-rbcL	trnG	trnLF
R. plicata	New Zealand	North Island	M.A.M. Renner		4 January 2002	AK280391	HM992000	HM992351	HM992437
R. pulchella	Australia	NSW	M.A.M. Renner	5230	11 April 2011	NSW875776	KF495319	KF495259	KF495378
R. pulchella	Australia	NSW	M.A.M. Renner	5231	11 April 2011	NSW875777	KF495320	–	KF495379
R. pulchella	Australia	NSW	M.A.M. Renner	5276	15 April 2011	NSW875822	KF495324	KF495263	KF495383
R. pulchella	Australia	NSW	M.A.M. Renner	5304	6 June 2011	NSW877196	KF495325	KF495264	KF495411
R. pulchella	Australia	NSW	M.A.M. Renner	5030	22 September 2010	NSW877631	KF495326	KF495265	KF495385
R. pulchella	Australia	NSW	M.A.M. Renner	5885	16 December 2011	NSW898672	KF495355	KF495294	KF495411
R. pulchella	Australia	NSW	H. Streimann	63817		EGR	HM992030	HM992380	HM992459
R. retroflexa	Australia	Qld	M.A.M. Renner	2049	10 July 2005	NSW872738	KF495318	KF495258	KF495377
R. retroflexa	Australia	Qld	M.A.M. Renner	6279	24 March 2012	NSW896660	KF495344	KF495282	KF495399
R. retroflexa	Australia	Qld	M.A.M. Renner	6311	24 March 2012	NSW896700	KF495345	KF495283	KF495400
R. retroflexa	Australia	Qld	M.A.M. Renner	6313	24 March 2012	NSW896703	KF495346	KF495284	KF495401
R. retroflexa	Australia	Qld	M.A.M. Renner	6582	8 April 2012	NSW898461	KF495353	KF495292	KF495409
R. retroflexa	Australia	Qld	M.A.M. Renner	6523	5 April 2012	NSW898764	–	KF495296	KF495413
R. retroflexa	Australia	Qld	M.A.M. Renner	6524a	5 April 2012	NSW898872	KF495357	KF495297	KF495414
R. retroflexa	Australia	Qld	M.A.M. Renner	6565	6 April 2013	NSW970436	KF495359	KF495300	KF495416
R. retroflexa	Cook Islands	Rarotonga	P.J. de Lange	CK183	11 July 2010	NSW973421	KF495365	KF495305	KF495421
R. retroflexa	Cook Islands	Rarotonga	P.J. de Lange	CK180	8 July 2010	NSW973422	KF495366	KF495306	KF495422
R. retroflexa	Fiji	Kadavu	M.A.M. Renner	5719	September 2011	NSW973391	KF495364	KF495304	KF495420
R. retroflexa	Fiji	Viti Levu	M.A.M. Renner	5428	31 August 2011	NSW889533	KF495332	KF495270	KF495391
R. retroflexa	Fiji	Viti Levu	M.A.M. Renner	5431	31 August 2011	NSW889536	KF495333	KF495271	KF495392
R. retroflexa	Fiji	Viti Levu	M.A.M. Renner	5606	4 September 2011	NSW973390	KF495363	–	KF495419
R. retroflexa	Fiji		S. & T. Pócs	03281/C		EGR	HM992035	HM992385	HM992464
R. retroflexa	Vanuatu		E.A. Brown	05/517		NSW	KF495317	KF495257	KF495376
R. sp.indet.	Fiji		E.A. Brown	05/362		NSW	KF495316	KF495256	KF495375
R. tasmanica	Australia	Tas.	M.A.M. Renner	5935	23 January 2012	NSW895266	KF495335	KF495273	KF440509
R. tasmanica	Australia	Tas.	M.A.M. Renner	5985	26 January 2012	NSW909280	–	KF495298	KF440511
R. tasmanica	Australia	Tas.	M.A.M. Renner	6013	27 January 2012	NSW970369	KF495358	–	KF440513
R. tasmanica	Australia	Tas.	M.A.M. Renner	5956	24 January 2012	NSW972574	KF495362	KF495303	KF440510
R. tasmanica	New Zealand	South Island	M.A.M. Renner	6188	17 February 2012	NSW895514	KF495338	KF495276	KF440548
R. tasmanica	New Zealand	South Island	M.A.M. Renner	6198	17 February 2012	NSW895583	KF495339	KF495277	KF440484
R. tasmanica	New Zealand	South Island	M.A.M. Renner	6224	18 February 2012	NSW895669	KF495341	KF495279	KF440549
R. tasmanica	New Zealand	North Island	M.A.M. Renner		15 October 2001	AK280184	HM991998	HM992349	HM992435
R. weymouthiana	Australia	Tas.	M.A.M. Renner	6052	31 January 2012	NSW898459	–	KF495291	KF495408
R. weymouthiana	New Zealand	South Island	M.A.M. Renner	6064	12 February 2012	NSW895339	KF495336	KF495274	KF495394
R. weymouthiana	New Zealand	South Island	M.A.M. Renner	6201	17 February 2012	NSW895586	KF495340	KF495278	KF495396

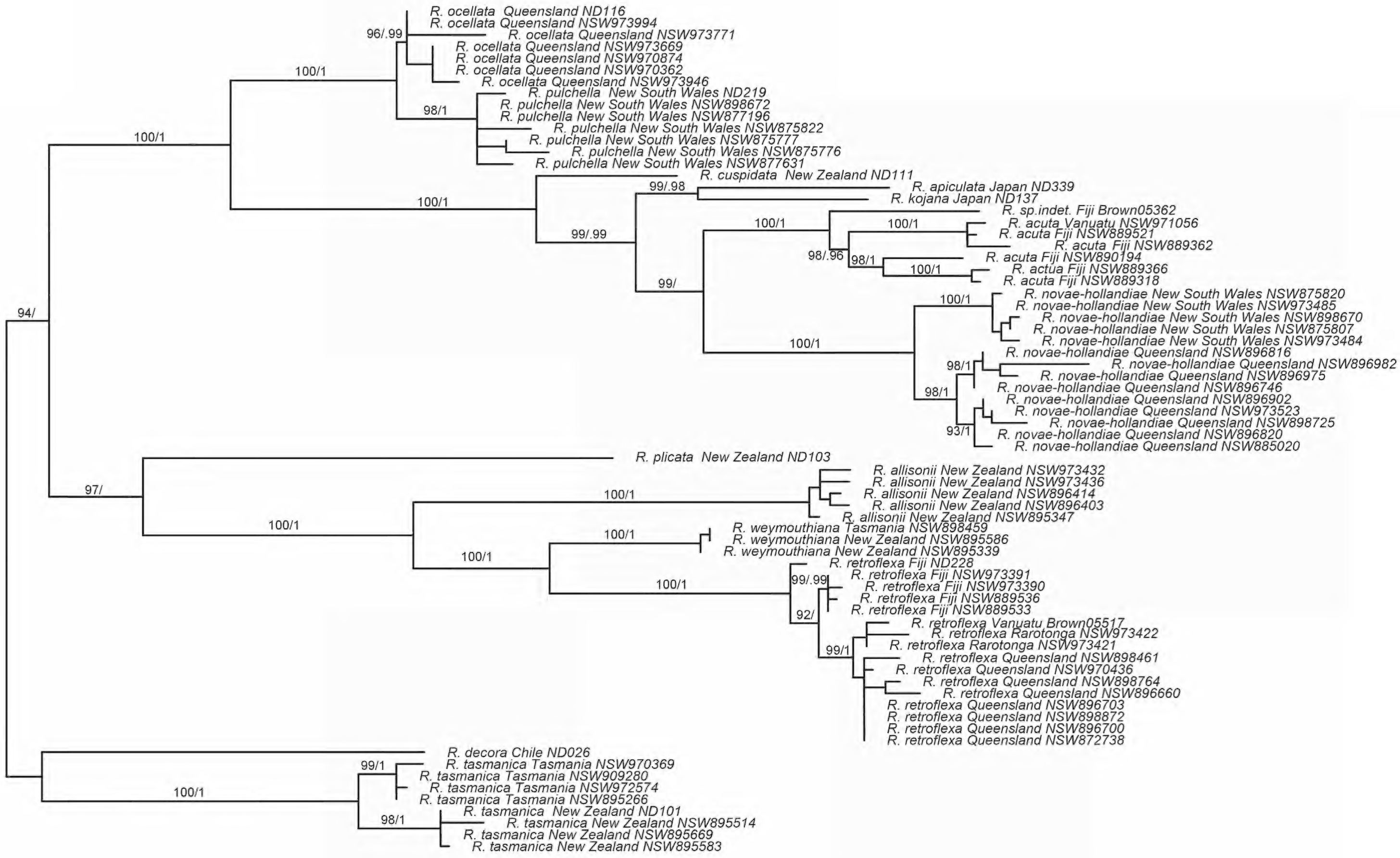

Fig. 1. Most likely tree reflecting relationships among individuals of *Radula* subg. *Odontoradula* included in this study. Numbers above branches are ultrafast bootstrap values from iQTree and posterior probability from BEAST.

Generalised mixed Yule coalescent (GMYC) analysis

Both the single and multiple threshold models were more likely than the null model of uniform (coalescence) branching rate (single: LGMYC = 552.9 vs. L0 = 546.3, 2DL = 26.1, P = 0.0014; multiple: LGMYC = 554.4 vs. L0 = 546.3, 2DL = 32.2, P = 0.0003). The multiple-threshold model provided a slightly better fit 2DL = 3.0. The single model fitted a switch resulting in 14 maximum likelihood (ML) clusters (confidence interval (CI: 7–14) and 21 ML entities (CI: 11–25). The multiple threshold model fitted three switches, resulting in 13 ML clusters (CI: 10–13) and 21 ML entities (CI: 14–25). The interpretation of geographic clades within *R. tasmanica* resulting in the only grouping difference between the two models, in the single threshold model interpreted these were interpreted as a phylogenetic divergence, but as coalescent branching in the multiple model. Both single and multiple threshold models identified three phylogenetic lineages within *R. novae-hollandiae*, one from south-east Australia, and two from the Wet Tropics of north east Queensland.

Fixed differences.

The number of fixed differences between individuals of *R. novae-hollandiae* from Queensland (=*R. tonitrua*) and New South Wales was 10, one more than separates *R. ocellata* and *R. pulchella*. The average number of differences between all pairs of individuals was slightly more than 15 in both species (Table 2).

Table 2. Number of fixed differences among sister lineages: n, the number of individuals included; k, the average number of nucleotide differences among individuals within populations; Mutations, the number of variable sites within species or populations. Differences are the number of fixed differences between individuals of each species or population pair, while the values in parentheses show the average number of differences between all pairs of individuals from each population.

		n	k	Mutations	Differences
R. tonitrua	Queensland	9	5.778	17	10 (15.6)
R. novae-hollandiae	New South Wales	5	1.6	4	
R. ocellata	Queensland	4	6	9	9 (15.3)
R. pulchella	New South Wales	9	3.6	12	
R. tasmanica	New Zealand	3	3.3	5	13 (15.2)
	Tasmania	2	1	1	

Discussion

Individuals of *Radula novae-hollandiae* from north-east Queensland and south-east Australia form two reciprocally monophyletic lineages which, in most analyses, are objectively diagnosable as two (or more) separate species. Improved modelling of sequence evolution, compared to Renner *et al.* (2013a), did not alter tree topology or branch lengths significantly, with the exception of the relationships between *R. decora* and *R. tasmanica* and the remainder of the subgenus in the ML tree. Despite these differences in topology within the MCC tree (see Fig. 2), the same groups were returned by objective species delimitation methods. The GMYC method is known to over-split entities (Luo *et al.* 2018), and this seems to have occurred in our analysis for *R. retroflexa*, *R. tasmanica*, *R. ocellata*, and also the Queensland lineage of *R. novae-hollandiae*. The depth of phylogenetic divergence, and number of fixed differences separating northern and southern lineages of *Radula novae-hollandiae* are both comparable with those separating *Radula pulchella* and *R. ocellata*, two sister species the latter of which was recognized on the basis of subtle, fixed, morphological differences from the first. These differences, associated with the presence of small accessory teeth around the lobule apex, were subsequently confirmed as reflecting a phylogenetic divergence by molecular data (Renner *et al.* 2013a). In contrast, the divergences between the northern and southern lineages of *R. novae-hollandiae* are shallower than those in *R. tasmanica*, which was interpreted, we believe correctly given the shared morphology of plants on both sides of the Tasman Sea, as within-species branching in the multiple threshold model. Northern and southern lineages of *R. novae-hollandiae* were not recognized as distinct by Renner *et al.* (2013a) because no morphological differences between northern and southern populations were detected by that study, hence *R. novae-hollandiae* appeared, like *R. tasmanica*, to present a case where geographically correlated divergences were possessed by single morphological entities. Subsequent investigation has demonstrated that this interpretation of morphological variation was incomplete, and that northern and southern lineages are morphologically diagnosable, on the basis of characters associated with reproductive structures generally considered critical for species circumscription within subg. *Odontoradula*, and *Radula* more broadly, in addition to lobule shape and propensity to asexual reproduction. A consistent interpretation of the molecular and morphological evidence, also compatible with overarching theory, is that the northern lineage of *R. novae-hollandiae* in the Wet Tropics

Bioregion comprises a new, undescribed species. *Radula novae-hollandiae,* in turn corresponds to the south-eastern lineage, from which the type specimen was derived. A single plant from the south-eastern lineage was the basis for the description of *Radula novae-hollandiae* in Renner *et al.* (2013a), and we refer readers there for a reasonably comprehensive description of it.

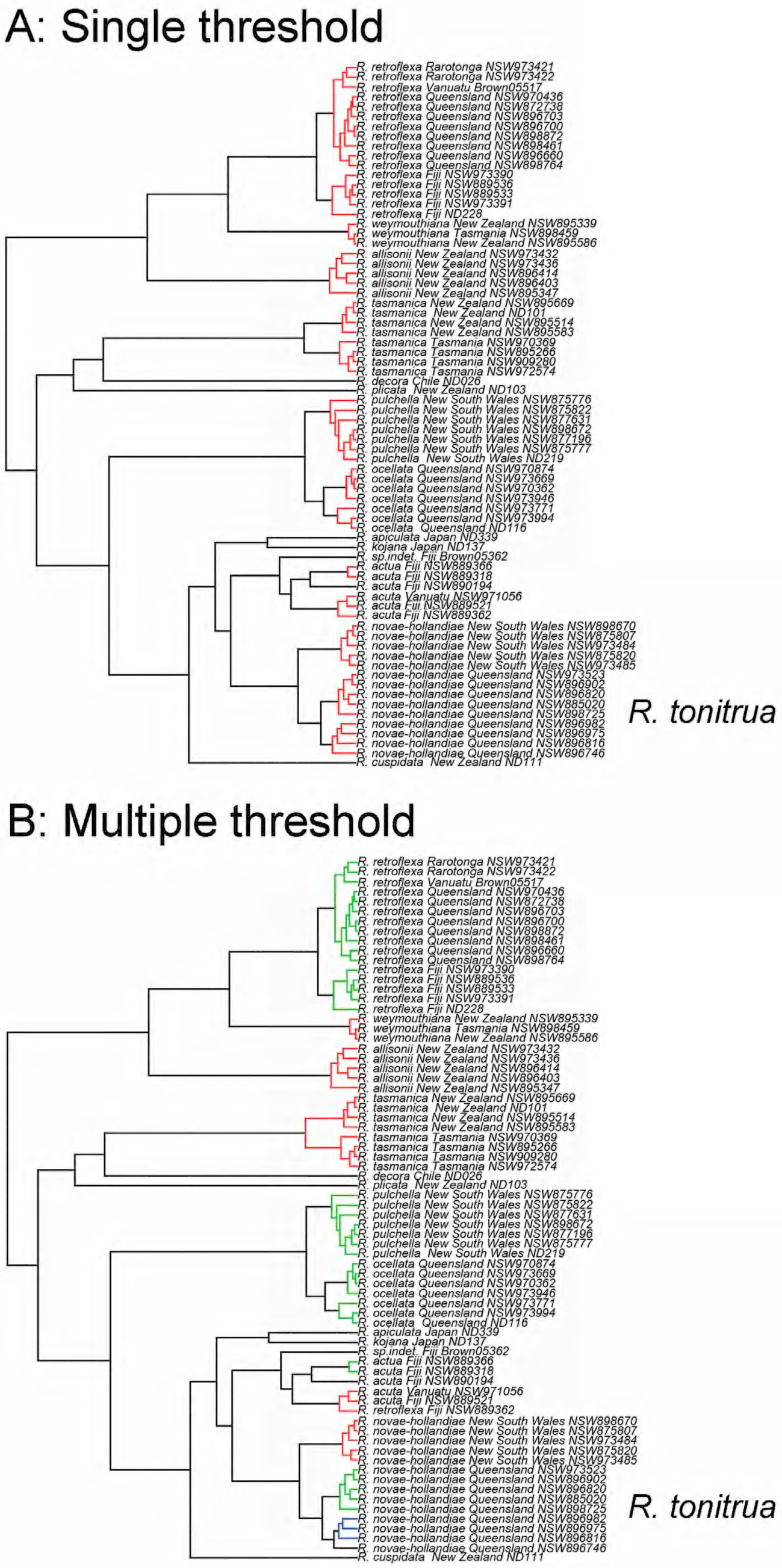

Fig. 2. GMYC analyses on MCC tree from BEAST, with phylogenetic branches in black, and coalescent branching in colour, as inferred using a single threshold between the two in A, and multiple, thresholds between the two in B, in which different colours are derived from different thresholds.

Taxonomic treatment

Radula tonitrua Pócs & M.A.M.Renner, *sp. nov*.

Diagnosis: *Radula tonitrua* is similar to *R. kojana,* but differs from by its much shorter perianth (1.6–2 mm long) and by the irregular shape and often much larger size (up to 120 µm long) of marginal gemmae, which in *R. kojana* are discoid or globular, usually not larger than 20 µm in diameter. The leaves of *R. kojana* are more concave and have a silky shine, which is not the case in *R. tonitrua.* It is similar in leaf and perianth shape to *R. novae-hollandiae* but separated by the presence of abundant marginal gemmae, which are not common in that species. *Radula tonitrua* differs from both by its stem medulla only 5 cells high and 6 cells wide, consisting of larger cells (10–20 µm in diameter).

Type: Australia: Queensland, Paluma Range State Forest 1.5 km NW of Paluma settlement. Birthday Creek, in the experimental area of James Cook University Tropical Biology Department. On *Abrodictyum obscurum* (Blume) Ebihara & K.Iwats. filmy fern leaves in wet, notophyll vine forest among boulders near the streamlet. At 840–870 m elevation, 18°59,\'9'S, 146°10'7–8'E *S. & T. Pócs 01121/AW,* accompanied by *A. Cairns, E.A. Brown & Ch. Cargill*, 20 June 2001. (holo: EGR, including 2 portions mounted on microslides; iso: BRI, CANB).

Description: (from the holotype). Epiphyllous (other specimens also lithophytic), forming loose mats, appressed to filmy fern leaves. Live plants dark green, pale green or brownish in herbarium. Shoots uni- to bipinnately branched, 0.6–1.0 mm, at the female perichaetium up to 1.5 mm wide. Stems in cross section ellipsoid, 50–100 µm (in average 5 cells) high and 60–120 µm (in average 6 cells) wide, constituted by 15–19 pale brown to rusty pigmented cortical cells, 20–40 µm long and 12–25 µm in diameter and 22–25 medulla cells, 10–20 µm in diameter, with pale yellow or colourless walls. All stem cells have evenly thickened (2 µm) walls except for the outermost wall of cortical cells (up to 3 µm thickness). Leaf insertions reach the midline of dorsal stem side but leave free 1–2 ventral cortical cell rows.

Leaf lobes asymmetrically ovate, somewhat falcate or deflexed, with obtuse to acute apex, 400–560 µm long and 250–300 µm wide on the main stem and 350–450 µm long and 200–320 µm wide on branches. Leaf lobes dorsally cover partially the stem, leaving free a zig-zag shaped zone in the lower part of stem, more imbricate upwards. Median lobe cells isodiametric polygonal, 19–25 µm in diameter, apical and marginal cells 12–16 µm. Cell walls evenly thin, with small triangular trigones. Leaf cell surface smooth. Lobe margins smooth to crenulate by bulging cells, often indicating origin of developing gemmae. Irregular shaped discoid or ribbon-like (sometimes bifurcate) gemmae copiously develop on the leaf margin (including perichaetial leaves and rarely the perianth mouth). In exceptional case the half surface of lobe is converted to gemmae or in other cases no gemmae develop at all. The gemmae are varied in size, consisting of a few to very many cells, in cases of ribbon-like ones up to 120 µm (12–15 cells) length and 50 µm (5–8 cells) width, uni- or rarely multilayered. The lobules rectangular, rhombic or triangular ovate, 1/3 to ½ length of the lobe, flat to slightly inflated in their postical half with obtuse to rounded apex. Angle between postical lobe margin and keel 130–140°. Interior lobule margin free from 1/10 to 1/4 of its length, the fused part straight, parallel to stem. Lobule cells similar to those of the lobe. Rhizoids of 8–10 µm of width, rare, develop from the slightly emergent lobule centre, pale brown, arranged in straight parallel bundles.

Perichaetium consists of 1–2 pairs of female bracts, which are much larger than ordinary leaves, up to 1000 µm length and 480 µm width, with acute apex, smooth or sometimes irregularly lobulate margin and triangular lobules of half lobe length. The angle of their postical margin to the stem is 155–170°. Cells and gemmae are similar to those of normal leaves. Mature perianth 1600–2500 µm long, at the mouth 500–600 µm wide, labia plane with gently undulate margin, unistratose in the upper third, conical in the upper two third tapering into the tubular stem perigynium of 250 µm width. In the perianth a young sporophyte was observed with cylindric capsule. Figs 1, 2.

Etymology: We understand that the name of type locality: Paluma State Forest, Paluma Range and Paluma National Park came from an aboriginal language in which "paluma" means thunder. Its Latin equivalent is "tonitrua", from which the species' binomial name is derived.

Additional specimens examined: Australia: Queensland, Paluma Range State Forest 1.5 km NW of Paluma settlement. Birthday Creek, 18°59'9'S, 146°10'7–8' E. 20 June 2001, *S. & T. Pócs 01121/BC,* accompanied by *A. Cairns, E.A. Brown & Ch. Cargill* (BRI); Daintree National Park, Mount Lewis, headwaters of Leichhardt Creek flowing down SW flanks of summit, 16°35'02"S, 145°16'33"E, 1150 m, 27 Mar. 2012, *M.A.M. Renner 6366, V.C. Linis & E.A. Brown*, NSW896820; Daintree National Park, Coast Range, Little Falls Creek catchment, immediately above the coral fern patch on the Manjal Jimalji track from Karnak to rock pinnacle, ENE of spot height 1198 m, 16°23'43"S, 145°17' 57"E, 1030 m, 28 Mar. 2012, *M.A.M. Renner 6377, V.C. Linis & E.A. Brown*, NSW896827; Main Coast Range, 19 km NNW of Mount Molloy, 16°31'S, 145°16'E, 1200 m, 30 June

1984, *H. Streimann 30249*, CANB8408604; Daintree National Park, Mount Lewis, upper Leichhardt Creek catchment, 16°34'59"S, 145°16'31"E, 1180 m, 27 Mar. 2012, *M.A.M. Renner 6341, V. C. Linis & E.A. Brown*, NSW896746; Kauri Creek, Mount Haig Road, Lamb Range, 22 km NE of Atherton, 17°08'S, 145°36'E, 800m, 27 June 1984, *H. Streimann 29887*, CANB8408242; Wooroonooran National Park, Bellenden Ker Range, Mulgrave River catchment, track to Choorichillum from end of Gourka Road, 17°22'48"S, 145°47'14"E, 1020 m, 30 Mar. 2012, *M.A.M. Renner 6401, V.C. Linis & E.A. Brown*, NSW896902; Palmerston Highway, Massey Creek, 8 km E of Ravenshoe, 17°37'S, 145°33'E, 1070 m, 8 Dec. 1990, *J.A. Curnow 3904*, CANB9409858; Wooroonooran National Park, South Johnston River catchment, Maple Creek, 17°40'59"S, 145°42'10"E, 590 m, 5 Apr. 2012, *M.A.M. Renner 6514, E.A. Brown & V.C. Linis*, NSW898725.

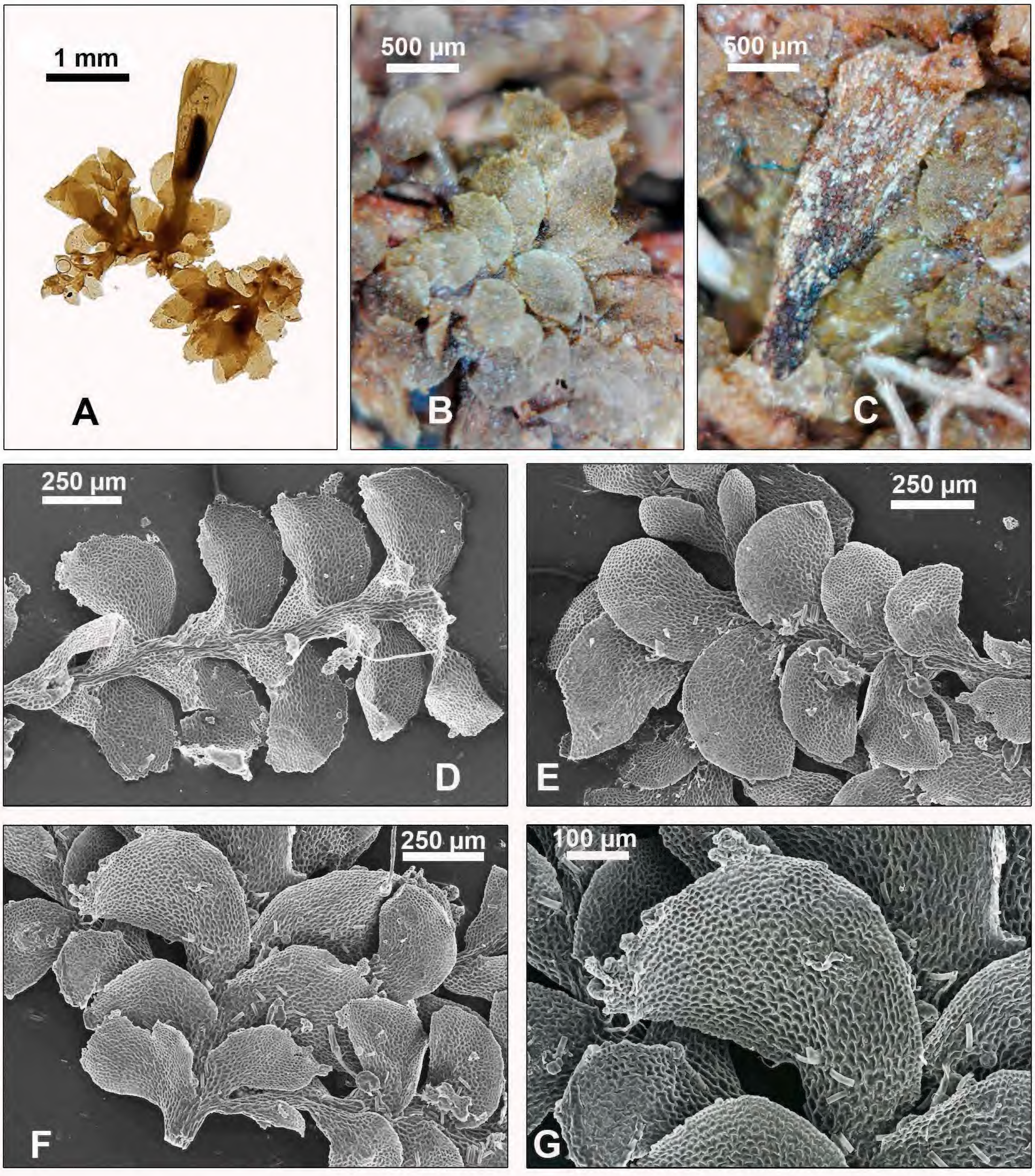

Fig. 3. *Radula tonitrua* A: Habit, ventral view. B, D, E and F: Habit, dorsal view. C: Mature perianth in dried herbarium material. G: Leaf, dorsal view. Images by T. Pócs from the holotype of *R. tonitrua*.

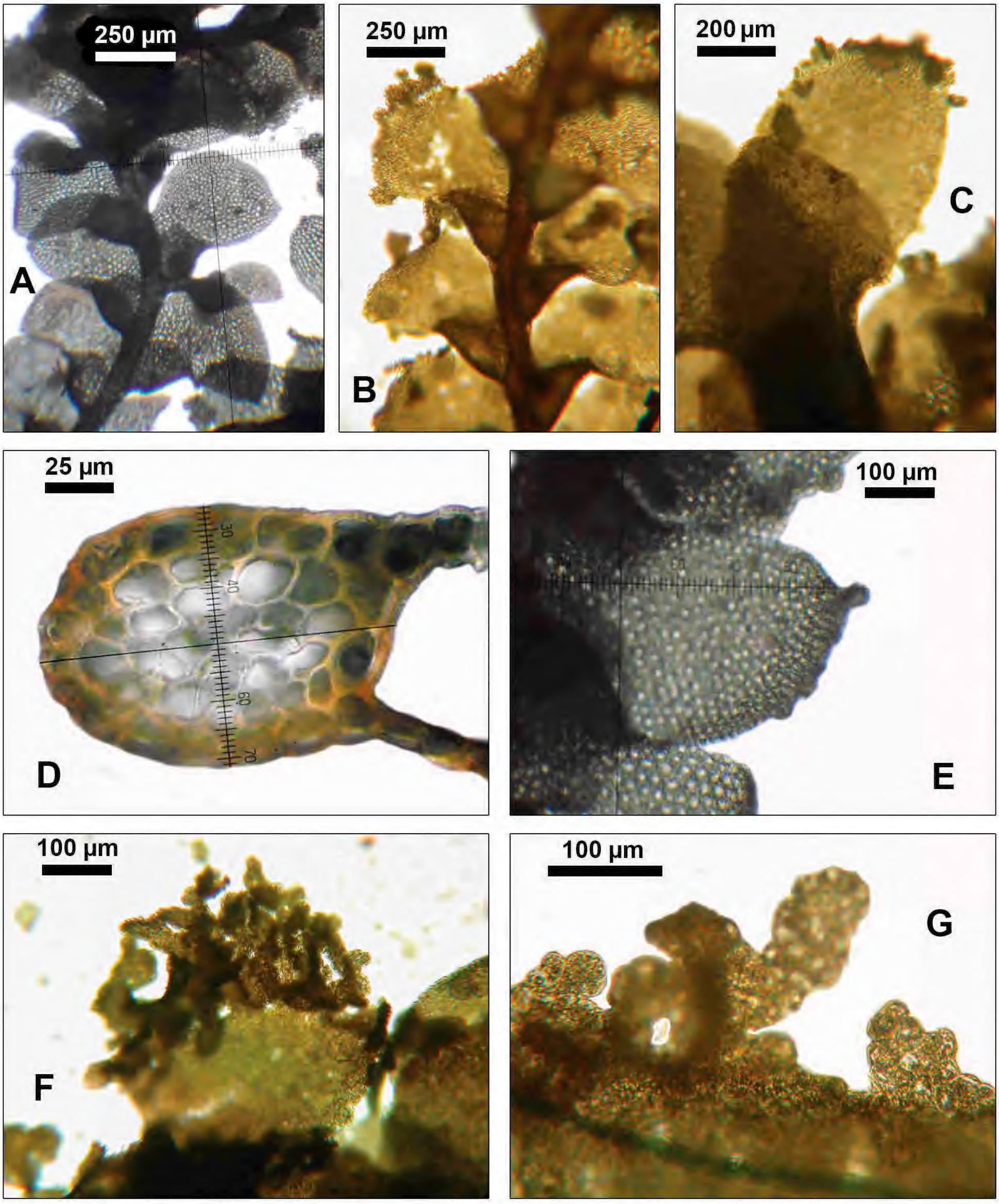

Fig. 4. *Radula tonitrua* A and B: Habit, ventral view. D: Leaf, ventral view. D: Cross section of main stem. E: Lobe margin with gemmae initials. E and G: Details of lobe margin with gemmae. Images by T. Pócs from the holotype of *R. tonitrua*.

Ecology. The specimens collected at the type locality were epiphyllous, growing on filmy fern leaves. The surrounding habitat is very wet with continuous high level of air moisture, near the cataracts of Birthday Creek. In other parts of the Wet Tropics Bioregion in north-eastern Queensland, *R. tonitrua* commonly grows in turfs on the sides of granite boulders, whether in association with permanent waterways or not. *Radula tonitrua* grows in association with a wide range of other lithophytic bryophytes, in particular *R. jovetiana* K.Yamada, *R. loriana* Castle, *R. myriopoda* M.A.M.Renner and *R. patens* K.Yamada, Lophocoleaceae spp., and Plagiochilaceae spp., and a variety of other mosses and liverworts, including Lejeuneaceae such as *Lopholejeunea muelleriana* var. *australis* (Steph.) B.Thiers & Gradst. (Renner *et al.* 2013a). Throughout its range, *R. tonitrua* inhabits wet tropical rainforests and montane rainforests from ~600 m to the tops of the highest peaks in the Wet Tropics, which range from 1200 to around 1600 m.

Revised couplets in key to species of *Radula* subg. *Odontoradula* (modified from Renner *et al.* 2013a)

4. Lobule margin irregularly crenulated because of bulging cells, lobules longitudinally rectangular. Apex of leaf lobules rounded to obtuse, apex of female bract lobes obtuse to acute..... 4a

   Lobule margin entire, lobules trullate. Apex of leaf lobes and female bract lobes rounded ..... *R. pugioniformis* M.A.M. Renner

4a. Perianths 1.6–2.0 mm long at maturity. Often with marginal gemmae on lobes of leaves and female bracts ..... *R. tonitrua* Pócs & M.A.M.Renner

   Perianths 3.8–4.5 mm long at maturity. Usually lacking gemmae..... *R. novae-hollandiae* Hampe

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References

Chernomor O, von Haeseler A, Minh BQ (2016) Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology* 65: 997–1008. https://doi.org/10.1093/sysbio/syw037

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772. https://doi.org/10.1038/nmeth.2109

Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7: 214. https://doi.org/10.1186/1471-2148-7-214

Drummond AJ, Ashton B, Buxton S, Cheung M, Cooper A, Heled J, Kearse M, Moir R, Stones-Havas S, Sturrock S, Thierer T, Wilson A (2012) Geneious v6.0. Available at http://www.geneious/com [Verified 24 February 2014]

Edgar RC (2004) MUSCLE: a multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics* 5: 113. https://doi.org/10.1186/1471-2105-5-113

Fontaneto D, Flot J-F, Tang CQ (2015) Guidelines for DNA taxonomy, with a focus on the meiofauna. *Marine Biodiversity* 45: 433–451. https://doi.org/10.1007/s12526-015-0319-7

Gernhard T (2008) The conditioned reconstructed process. *Journal of Theoretical Biology* 253: 769–778. https://doi.org/10.1016/j.jtbi.2008.04.005

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.

Hoang DT, Chernomor O, von Haeseler A, Minh BQ, L.S. Vinh LS (2018) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35: 518–522. https://doi.org/10.1093/molbev/msx281

Librado P, Rozas J (2009) DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* 25: 1451–1452. https://doi.org/10.1093/bioinformatics/btp187

Luo A, Ling C, Ho SYW, Zhu CD (2018) Comparison of methods for molecular species delimitation across a range of speciation scenarios. *Systematic Biology* 67: 830–846. https://doi.org/10.1093/sysbio/syy011

Minh BQ, Nguyen MAT, von Haeseler A (2013) Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution* 30: 1188–1195. https://doi.org/10.1093/molbev/mst024

Miller MA, Holder MT, Vos R, Midford PE, Liebowitz T, Chan L, Hoover P, Warnow T (2010) The CIPRES portals. Available at http://www.phylo.org [Verified 24 February 2014]

Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274. https://doi.org/10.1093/molbev/msu300

Paradis E, Claude J, Strimmer K (2004) APE: analysis of phylogenetics and evolution in R language. *Bioinformatics* 20: 289–290. https://doi.org/10.1093/bioinformatics/btg412

Pócs T, Cairns A (2008) Contributions to the bryoflora of Australia, III. The genus *Jubula* Dumort., with the description of *J. hutchinsiae* Hook. subsp. nov. *australiae* (Jubulaceae, Jungermanniopsida). *Nova Hedwigia* 86: 231–236. https://doi.org/10.1127/0029-5035/2008/0086-0231

Pócs T, Streimann H (2006) Contributions to the bryoflora of Australia, I. *Tropical Bryology* 27: 19–24. https://doi.org/10.11646/bde.27.1.4

Pócs T, Brown EA, Cairns A, Cargill DC, Pócs S (2012) Contributions to the bryoflora of Australia, III. The genus *Nowellia* Mitt. (Cephaloziaceae, Jungermanniopsida). *Acta Biologica Plantarum Agriensis* 2: 21–26. http://abpa.ektf.hu/uploads/papers/finalpdf/ABPA_2_from21to26.pdf

Pons J, Barraclough TG, Gomez-Zurita J, Cardoso A, Duran DP, Hazell S, Kamoun S, Sumlin WD, Vogler AP (2006) Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology* 55: 595–609. https://doi.org/10.1080/10635150600852011

Puillandre N, Lambert A, Brouillet S, Achaz G (2012) ABGD, automatic barcode gap discovery for primary species delimitation. *Molecular Ecology* 21: 1864–1877. https://doi.org/10.1111/j.1365-294X.2011.05239.x

Rambaut A, Drummond AJ (2009) Tracer v1.5. Available at http://tree.bio.ed.as.uk/software/tracer/ [Verified 6 March 2014]

Renner MAM, Devos N, Brown EA, von Konrat MJ (2013a) A revision of Australian species of *Radula* subg. *Odontoradula*. *Australian Systematic Botany* 26: 408–447. http://dx.doi.org/10.1071/SB13035

Renner MAM, Devos N, Brown EA, von Konrat MJ (2013b) New records, replacements, reinstatements, and four new species in the *Radula parvitexta* and *R. ventricosa* aggregates (Jungermanniopsida) in Australia: cases of mistaken identity. *Australian Systematic Botany* 26: 298–345. https://doi.org/10.1071/SB13027

Stech M, Quandt D (2010) 20 000 species and five key markers: the status of molecular bryophyte phylogenetics. *Phytotaxa* 9: 196–228. https://doi.org/10.11646/phytotaxa.9.1.11

Yamada K (1979) A revision of Asian taxa of *Radula*, Hepaticae. *The Journal of the Hattori Botanical Laboratory* 79: 201–322.

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A review of *Dendrobium kingianum* Bidwill ex Lindl. (Orchidaceae) with morphological and molecular-phylogenetic analyses

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Abstract

Populations of *Dendrobium kingianum* Bidwill ex Lindl. from near Newcastle, New South Wales to southern and central west Queensland and encompassing all regions of the distribution were studied using field observations, morphometric analysis and nrITS sequences. A total of 281 individuals were used to construct regional descriptions of *D. kingianum* and 139 individuals were measured for 19 morphological characters, and similarities and differences among specimens summarised using multivariate statistical methods. Patterns of morphological variation within *D. kingianum* are consistent with a single variable species that expresses clinal variation, with short-growing plants in the south and taller plants in the northern part of the distribution. The nrITS gene tree suggests two subgroups within *D. kingianum* subsp. *kingianum*, one comprising northern, the other southern individuals, which may overlap in the vicinity of Dorrigo, New South Wales. The disjunct *D. kingianum* subsp. *carnarvonense* Peter B. Adams in central west Queensland, which can be distinguished by a predominately subterranean habit and a narrower labellum midlobe, was resolved sister to *D. moorei* F.Muell., which renders *D. kingianum* paraphyletic in the nrITS gene tree, but this position was not supported. Regional descriptions documenting clinal variation are provided. All previously described varieties, including *D. kingianum* var. *pulcherrimum* Rupp, are colour and growth forms of *D. kingianum* subsp. *kingianum*.

Introduction

Dendrobium kingianum Bidwill ex Lindl. (sect. *Dendrocoryne*) is a lithophyte found mainly on the eastern seaboard in the northern half of New South Wales (NSW) and southern Queensland. There are also isolated and disjunct populations in inland central west Queensland. Across this broad distribution the species is variable in plant form and floral colour. *Dendrobium kingianum* was discovered by European explorers in the 1830s when opening up agricultural land north of Newcastle, and was described in 1844 by John Lindley from material sent by John Carne Bidwell, and named for Bidwell's friend Captain P.P. King of the Royal Navy. The collection location for type plants was not given but the description is consistent with those from the southern part of the range. Subsequently the known distribution was extended to the north as far as central Queensland. It has been widely cultivated in temperate zones. The species is of significant horticultural interest, and since the mid-20th century has been line bred and hybridised with other dendrobiums. There have been a number of taxa described, some separated at species level. This can create confusion for orchid hybrid registration.

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There are a small number of studies of chromosome counts (Adams 1992), pollination (Adams 1988, Adams and Lawson 1988) and fragrance biochemistry (Adams 1988, Adams and Lawson 1995). Molecular phylogeny reconstruction using nuclear ITS for the 12 species in sect. *Dendrocoryne* (Burke *et al.* 2008) resolved *D. kingianum* as sister to *D. speciosum*, a relationship also recovered using AFLP data by Simpson *et al.* (2018).

The aims of this paper are to quantify variation within *D. kingianum* based on morphological and molecular phylogenetic analysis from populations across the distribution. In particular we are interested in morphological evidence relating to the potential existence of more than one species. Clements and Jones (2002) proposed that *D. kingianum* be split into three separate species under *Thelychiton*, namely, *T. kingianus*, *T. pulcherrimus* and *T. carnarvonense*. Neither *Thelychiton* nor these species have been accepted by the World Checklist of Selected Plant Families (WCSPF), *Genera Orchidacearum* Vol. 6 (Pridgeon *et al.* 2014) or a review of the systematics of Dendrobiinae (Adams 2011). We then formalise the results of this investigation, in conjunction with a taxonomic review of *D. kingianum*.

Historical review of taxonomy

Dendrobium kingianum is a variable species. In the late 19th and early 20th centuries, varietal status was proposed for particular plants with distinctive features, often flower colour and plant habit e.g. *D. kingianum* var. *pallidum* F.M.Bailey, *D. kingianum* var. *silcockii* F.M.Bailey, *D. kingianum* var. *aldersoniae* F.M.Bailey and *D. kingianum* var. *album* Williams. In 1943, Rupp described *D. kingianum* var. *pulcherrimum* Rupp for very short plants with comparatively large flowers from the upper Hastings River in the southern part of the range, and noted that few variations of the species were sufficiently constant to warrant even varietal rank. A description of the historical varieties and a subspecies are given below with comments.

***Dendrobium kingianum* Bidwill ex Lindl.**

The protologue of *D. kingianum* (Lindley 1844) was based on a single cultivated plant shipped from Australia to England by J.C. Bidwill, purchased by the Loddiges brothers possibly in 1842 (Lindley 1845), and cultivated. The plant's pseudobulbs were 4–5 inches long, bearing two leaves, and two-flowered inflorescences.

> *D.* (*Desmotrichum*) *Kingianum*; pseudobulbis ovatis in collum longum extensis apice bioliis, foliis ovalibus emarginatis, pedunculo terminali (2-floro foliis aequali ?), sepalis ovatis mento emarginato, petalis obovatis apiculatis duplo brevioribus, labelli trilobi pubescentis laciniis lateralibus acutis intermedia paulo longiore transverse rhombea angulis lateralibus rotundatis apiculi acuto axi elevata trilineata apice tridentata.
>
> This curious epiphyte was bought by the Messrs. Loddiges at the sale of Mr Bidwill's New Holland Plants. It has pseudo-bulbs between four and five inches long, tapered from an ovate base into a very long and narrow neck, on the top of which stand two oblong emarginate dark-green rather wavy leaves. Between these is a flower-stalk having two pink flowers gaily spotted with crimson in the inside. It will probably flower more profusely when in better health, and will then be a plant of considerable interest.

The following year Lindley (1845) published a longer treatment of the plant, including a colour illustration, and noted three flowered inflorescences and four-leaved canes.

Mueller (1862) provided a description including the same characters as Lindley's, but based on a specimen collected by Charles Stuart from the Severn River in New England, presumably from high altitude on the edge of the New England escarpment, where *D. kingianum* is common even today:

> Caulibus breviusculis pauciarticulatis basi sensim incrassatis, foliis 2-4 terminalibus ovato-lanceolatis, corymbo terminalia pauciflora, floribus roseo-purpureis, sepalis semilanceolato-ovatis petala ovato-lanceolata aequantibus, labello sepalis subaequilongo albo vittis purpureis striato trilobo, lobis lateralibus deltoideis, medio subreniformi apiculato integro, earinis tribus flavis usequ ad basin lobi medii extensis.
>
> In Nova Anglia haud procul a fluvio Severn. C. St.
>
> In indice orchidearum horti Schilleriani sequentes species Dendrobii Novo-Hollandicas nuperius enumerantur: D. calamiforme Lodd., D. lineolatum H.G.Rchb. (D. teres Lindl. nec R.Br.)
>
> Nondum vidi Dendrobium monoliforme (McLeay inedit), quod a viro reverendo R.L. King prope sinum Botany Bay in rupibus muscosis repertum et raritate minutie sicut caulibus subtiliter moniliformibus insigne dicitur. Hoc Forsan Bolbophyllis adscibendum est.

Bentham's description of *D. kingianum* in *Flora Australiensis* (1873: p. 280) encompassed more natural variation, with stems 3–6 inches tall, and 1–3 inflorescences per pseudobulb. He suggested Bidwill's plant may have come from Moreton Bay, and cited specimens collected at 'Biron' (possibly Byron Bay) by Leichardt, and at New England collected by C. Stuart, so encompassing the elevational range occupied by the species:

> Stems usually 3 to 6 in. high, striate with prominent angles, thickened at the base. Leaves at the summit of the stem 3 to 5, lanceolate or oblong-lanceolate, acute, 3 to 4 in. long. Racemes within or above the leaves 1 to 3, longer than the leaves. Flowers of a reddish purple, on pedicels of 1/4 to 1/2 in. Bracts very small. Sepals broadly lanceolate, the lower ones much falcate, 4 lines long in some specimens, fully 5 in others. Petals about as long, but narrower. Spur conical, slightly incurved, about 3 lines long. Labellum not much shorter than the sepals, not undulate, the lateral lobes very prominent, almost oblong, obtuse, the middle lobe scarcely longer, but very broad, almost reniform, the disk with 3 raised lines or plates extending to the base of the middle lobe, but not beyond.—Bot. Mag. t. 4527; F. Muell Fragm. iii. 60.
>
> Queensland, Morton bay ? Bidwill.
>
> N. S. Wales. On rocks and trees, Biron, *Leichhardt;* New England, *C. Stuart.*

The early descriptions do not encompass the full range of variation within *D. kingianum* there being, for example, no information about the number of flowers per raceme and little information about the colour or shape of the labellum.

Dendrobium kingianum var. _pallidum_ F.M.Bailey

A new variety of *D. kingianum* was described, in somewhat unusual circumstances, by F.M. Bailey. The summary of Bailey's paper presented to the Queensland Philosophical Society and printed in *The Brisbane Courier* (Anonymous 1883) actually fulfilled the requirements for valid publication of *D. kingianum* var. *pallidum*, a fact evidently of some embarrassment to Bailey, who noted in his more formal description of the taxon the following year (Bailey 1884) that the species was 'published in a newspaper report of the last meeting of the Queensland Philosophical Society, a publication scarcely meeting the requirements of scientific currency'. This was not the first orchid validly published in a newspaper. *Dendrobium fairfaxii* F.Muell & Fitzg. had been described in *The Sydney Mail*, the weekly edition of *The Sydney Morning Herald*, in 1872, and *D. falcorostrum* Fitzg. had been described in the *Sydney Morning Herald* in 1876.

Bailey (1884) described his new variety as follows:

> Stems clustered, often forming broad dense matted masses of several feet in diameter, the height of stem from 2 to 4 inches, slender except the base which is enlarged into pseudobulbs, all more or less covered by the torn bases of old leaves. Leaves 2 or 3 somewhat thin, 2–3 inches long, and about 1/2 inch broad near the base, oblong-lanceolate. Racemes slightly exceeding the leaves, slender and bearing about three or four white or lilac stained flowers.
>
> Habitat: On rocks Main Range, collected by B. Crow and C.H. Hartmann.

As first proposed, *Dendrobium kingianum* var. *pallidum* differed from *D. kingianum* var. *kingianum* by its smaller stature, pseudobulbs that formed dense masses, and by the white or pale pink colour of the flowers. However, Bailey later provided a slightly different description for his *D. kingianum* var. *pallidum*, including much taller plants, in the *Queensland Flora* (Bailey 1902):

> The clustered stems weaker than the typical form, often densely matted together and thus forming large patches on the rocks. Stems 2 to 9 inches high, the base enlarged in pseudobulbs. Leaves of a thin texture 2 to 3 inches long, about half an inch broad near the base, and tapering towards the apex. Racemes slightly longer than the leaves, bearing 3 or 4 pale lilac stained flowers.

This broadened description suggests that Bailey had seen a range of plants of different cane lengths between 1884 and 1902, and therefore indicated the range 2–9 inches in the later description. This effectively left flower colour as the only feature distinguishing *D. kingianum* var. *pallidum*.

Dendrobium kingianum var. _album_ B.S.Williams

A pure white form of what was thought to be *D. kingianum* was described and illustrated in Warner and Williams (1888), with the figure drawn from a plant that flowered in the collection of A.H. Smee, The Grange, Carshalton, Surrey, England. The flower spike bore 20 large white flowers whose labellum was freckled with a few reddish-brown lines and dots. The inflorescence length, flower number, labellum marking, and growth form all demonstrate that the plant was in fact *D.* × *delicatum* (F.M.Bailey) F.M.Bailey. Many white-flowered plants of *D. kingianum* are cultivated under the name *D. kingianum* var. *album*, but this name applies to *D.* × *delicatum* and not *D. kingianum*. Pure white and off-white flowers of *D. kingianum* with a trace of pale mauve are scattered throughout the distribution range in all growth forms.

Dendrobium kingianum subvar. _pallidum_ J.H.Veitch

Veitch in his *Manual of Orchidaceous Plants* fulfilled, perhaps inadvertently, the requirements for valid publication of a 'subvariety' of *Dendrobium kingianum* called 'pallidum' with 'white flowers with a few purple

stripes on the labellum' (Veitch 1887). No type specimen was indicated, and none has been found for this brief description. *Dendrobium kingianum* subvar. *pallidum* may resemble, or be an example of the colour form known as 'silcockii', the flowers are off-white in colour with a few faint streaks of pale mauve in the labellum.

***Dendrobium kingianum* var. *silcockii* F.M.Bailey**

This name is widely used today in reference to plants with white tepals which contrast with the purple coloured labellum. *Dendrobium kingianum* var. *silcockii* was described as follows (Bailey 1902):

> Stem and leaves firm as in the typical form. Flowers pure white except the labellum and of thick substance. Pedicels white 1/2 inch long. Ovary green, two lines long. Dorsal sepal five lines long three lines broad., cymbiform, lateral ones broad, falcate, from point to point seven lines quite enclosing the elongated base of the column (spur). Petals long as dorsal sepal but not so broad, incurved and meeting over the column. Labellum about as long as the sepals, lateral lobes spreading, pointed at the ends and reaching above the column, marked with lilac lines, middle lobe broadly cordate, apiculate, lilac lined with white. The disk bearing three thick ridges ending in points at the base of the middle lobe. Column thick and short. Anther lid ciliate in front. Pollen masses amber coloured.

'Silcockii' has been used for colour forms with pure white sepals and petals, and a purple and white speckled or patterned labellum. It is sometimes applied to flowers that are a pale mauve with purple speckled lip, but it should be reserved for flowers with white tepals, as per the protologue. Plants with 'silcockii'-type flower colouration occur sporadically in many areas of the distribution range with a wide variety of growth forms and variable floral size, shape and other characteristics (Adams and Lawson 1995). It is therefore a colour form only. Selfings and sibling crosses breed plants with flowers that have shades of mauve, mainly pale and only occasional true 'silcockii', indicating the presence of genes for mauve, which are expressed in 'silcockii' itself.

***Dendrobium kingianum* var. *aldersoniae* F.M.Bailey**

Bailey (1905) provided the following brief description:

> Habit of the typical form. Flowers fragrant as in other forms, pure white except sometimes a very faint purple stain on the back of the sepals; and the labellum very faintly dotted with purple, the disk plates yellowish.
>
> Collected in the Blackall Range. Mrs. G.W. Alderson.

The original material has not been found. The original spelling by Bailey was *aldersonae,* subsequently corrected to *aldersoniae* by other authors. There is no evidence to suggest that this is a distinct variety. The description could match plants from many parts of the distribution range.

***Dendrobium kingianum* var. *pulcherrimum* Rupp**

Rupp (1943) described *D. kingianum* var. *pulcherrimum* as

> Pseudobulbs crowded, all short, not exceeding 9cm. Leaves as long as the pseudobulbs, tinged with red. Flowers comparatively large, the sepals and petals deep mauve. Labellum white on the undersurfaces and the margins'.

He commented 'There are many varieties in this species chiefly of colour, but few appear to be sufficiently constant to warrant varietal rank.' This variety was described from plants collected in the Upper Hastings River with congested short (<9 cm) pseudobulbs and relatively large, deep mauve flowers with a white margin. Other treatments (Dockrill 1992, Upton 1989) have listed the variety, recording 1–3 or few flowers per raceme, blue-green leaves, with a distribution from the Macleay River down to the southern limit of the species.

Plants agreeing with this description are seen occasionally in the Hastings River region and less commonly elsewhere (see descriptions for Hastings, Comboyne and Coffs Harbour/Dorrigo). Although plants are generally short (<11 cm), there is a wide range of floral colour, white-purple, flowers per raceme (2–8), midlobe shapes and leaf lengths. Grey-green leaves are a feature of the southern region in most populations, and very few plants in each population could be ascribed to Rupp's description. In this study, three plants meeting the description were recorded in the northern part of the range, and eight plants meeting the description from the three southern-most regions. At Bulahdelah, approximately the southern limit, plants are very short (4–8 cm), may have 1–5 flowers which are small, not larger in all aspects, and of a pale mauve, rarely if ever deep purple, and not meeting Rupp's description. The populations in the Upper Hastings contain significant numbers of large mauve flowering forms mixed with smaller and paler flowering individuals, with a wide range of stem heights, mostly longer than seen in *D. kingianum* var. *pulcherrimum*.

***Dendrobium kingianum* subsp. *carnarvonense* Peter B. Adams**

This subspecies was described in Adams and Lawson (1995) for unusual forms of *Dendrobium kingianum* growing in disjunct sandstone gorges of Central Queensland, between the Carnarvon region and Isla Gorge, usually in secluded, shaded situations near streams.

The plants have slender pseudobulbs, up to 15 cm long, the older ones and lower portions of newer pseudobulbs covered by decomposing sandstone and leaf litter, the upper portions emergent and bearing frequent aerial growths, with small flowers having a rounded outline, 1.6 by 2.2 cm in vertical and horizontal dimensions. The forelobe and midlobe of the labellum are unusually curved to form a narrow open tube approximately 0.35 – 0.5 cm wide, and the labellum callus is green without any raised keels. Subspecies rank was chosen for these plants to reflect their geographic isolation, and the relatively subtle nature of differences from other *D. kingianum*.

Material and Methods

Field Survey and Population Sampling

Populations in all regions of the distribution (Fig. 1) were studied in the flowering season during September to October, between 1980 and 2019. Plants in 52 main locations were selected to represent the variation in each location (Table 1). Numerical and morphological data from 281 specimens was obtained from wild plants *in situ* and used to describe plants from regions 1–8.

Table 1. Vouchers and sources for sequences used in nrITS gene tree reconstruction.

New South Wales	Subspecies	Region	Coordinates
Mt Alum	kingianum	1	32°24′S 152°13′E
Middle Brother	kingianum	3	33°15′S 149°17′E
Comboyne	kingianum	3	31°36′S 152°28′E
Yarras	kingianum	3	31°26′S 156°20′E
Haystack/Little Nellie	kingianum	3	31°24′S 152°30′E
Jollynose	kingianum	3	31°35′S 152°47′E
North of Wauchope	kingianum	3	31°28′S 152°43′E
Cairncross	kingianum	3	31°20′S 152°40′E
Hastings	kingianum	3	32°24′S 152°13′E
Kundebung	kingianum	3	31°12′S 152°51′E
No. 1626 Gibraltar Range	kingianum	5	29°32′S 152°17′E
Dorrigo	kingianum	4	30°20′S 152°43′E
Russell's Red	kingianum	2	32°02′S 151°57′E
Gibraltar Range/Hanging Rock Station	kingianum	4	29°32′S 152°17′E
Busby's Flat	kingianum	6	29°02′S 152°50′E
Grafton	kingianum	4	29°40′S 152°56′E
Coledale	kingianum	5	34°17′S 150°57′E
Clouds Creek	kingianum	4	30°05′S 153°37′E
Sherwood Road, Coffs Harbour	kingianum	4	30°06′S 153°03′E
Korora	kingianum	4	30°14′S 153°06′E
Stanton, Bucketts	kingianum	2	32°01′S 151°57′E
Farley, Bucketts	kingianum	2	32°01′S 151°57′E
Bucketts	kingianum	2	32°01′S 151°57′E
Benny's Tops	kingianum	2	32°01′S 151°07′E
Bald Rock	kingianum	5	28°57′S 152°01′E
Rocky River	kingianum	6	29°02′S 152°29′E
Boonoo Boonoo	kingianum	6	28°56′S 152°06′E
Lamington	kingianum	6	28°15′S 153°05′E
Tunglebung	kingianum	6	28°50′S 152°41′E
Glenreagh Ridge	kingianum	5	30°03′S 152°59′E

New South Wales	**Subspecies**	**Region**	**Coordinates**
Stewart Creek, Lansdowne	kingianum	3	31°46′S 152°32′E
Glenreagh	kingianum	3	30°03′S 152°59′E
Dungog	kingianum	2	32°24′S 151°45′E
Rowley's Ridge, Gloucester	kingianum	2	32°01′S 151°07′E
Paterson	kingianum	1	32°35′S 151°36′E
Morgan's Camp	kingianum	5	34°17′S 150°57′E
Pinnacle	kingianum	6	28°26′S 153°06′E
Plants Queensland			
Tarlington 1	kingianum	6	28°03′S 153°14′E
Tarlington 2	kingianum	6	28°03′S 153°14′E
Main Creek	kingianum	6	28°07′S 153°11′E
Coongara	kingianum	7	25°40′S 151°59′E
Mt. Tamborine	kingianum	6	27°56′S 153°11′E
Tallai	kingianum	6	28°04′S 153°19′E
Cedar Creek	kingianum	6	27°49′S 153°10′E
Carnarvon Gorge	carnarvonense	8	25°03′S 148°13′E
Carnarvon Gorge 2	carnarvonense	8	25°03′S 148°13′E
Robinson Gorge	carnarvonense	8	25°17′S 149°08′E
Mt. Tavingah	kingianum	7	26°25′S 152°18′E
Mothar Mountain	kingianum	7	26°14′S 152°46′E
Nimbin	kingianum	6	28°36′S 153°11′E
Ngun Ngun	kingianum	7	26°54′S 152°58′E
Beerwah	kingianum	7	26°15′S 152°57′E

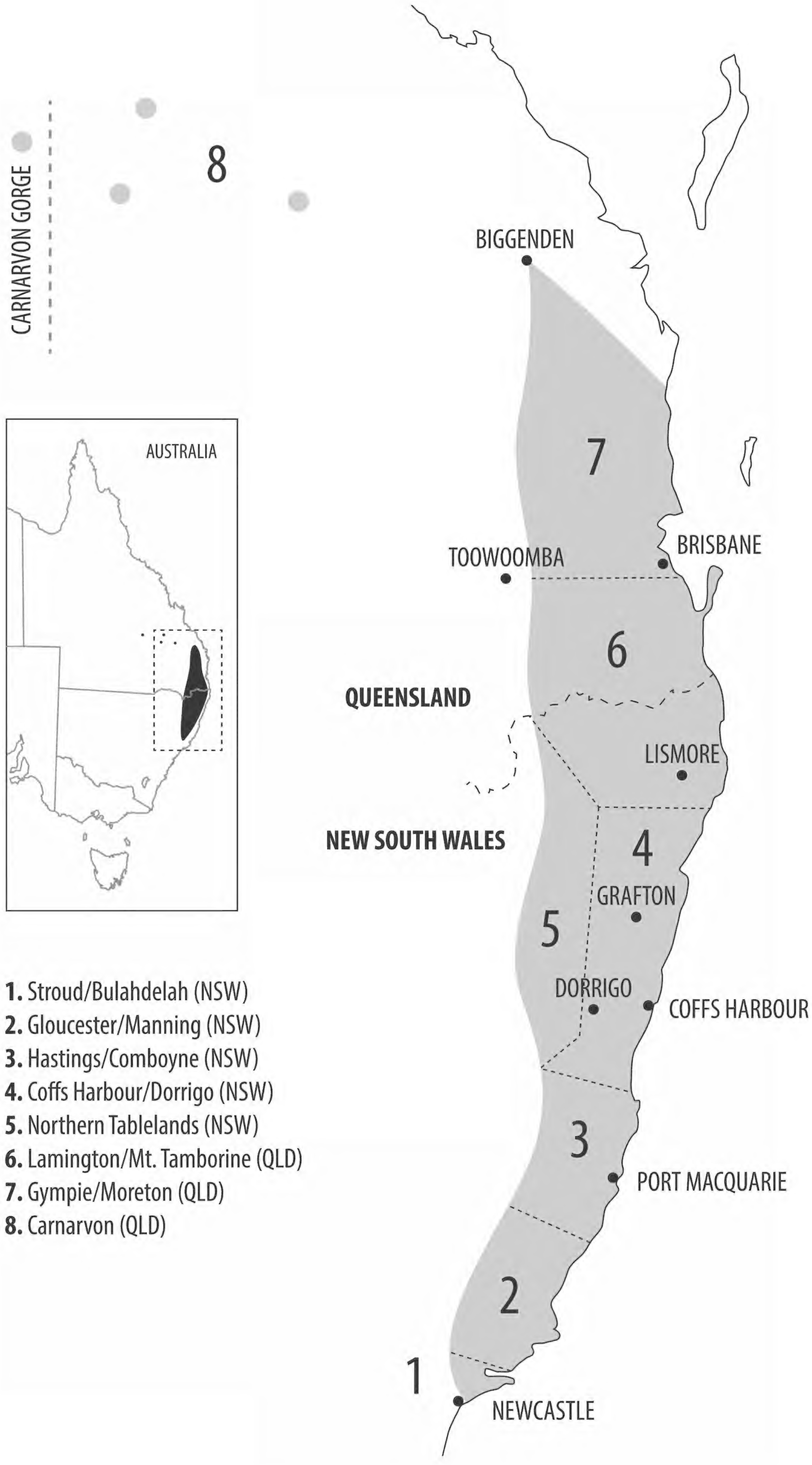

Figure 1. Distribution of *Dendrobium kingianum* showing regions used as a factor in the morphological analysis.

Molecular phylogenetic analysis

New sequences for the nuclear internally transcribed spacer (nrITS) were generated from eight *D. kingianum* samples using the extraction, PCR, and sequencing methods described by Burke *et al.* (2008). Consensus sequences were assembled using Sequencher v.4.0 (Gene Codes Corporation, U.S.A.) and manually aligned using SeA1 Sequence Alignment Editor V. 2.0a11 (Rambaut 1996). These were combined with 82 published nrITS sequences from *Dendrobium* downloaded from GenBank, representing 39 species with an emphasis on the Australian region. In total fourteen samples of *D. kingianum* were included, so that all major regional variants (Adams and Lawson 1995) were represented. A number of accessions from *D. speciosum* J.Sm. and *D. tetragonum* F.Muell. were included from those available on GenBank for purposes of comparing the levels of nrITS haplotype diversity within each species. Voucher details and GenBank accession numbers are provided in Table 2. The sequences were aligned by MUSCLE, as implemented in Geneious Prime 2020.0.5 (BioMatters Ltd), with all default options. The MUSCLE alignment was then manually edited to compensate for localised over alignment of some indels.

We estimated a nrITS gene tree as a basis for inferring the relationships of *Dendrobium kingianum*, and variation within *D. kingianum*. The optimal substitution model was estimated with jModelTest 2.1.10 (Darriba *et al.* 2012). We estimated the most likely nuclear ITS gene tree and branch support in a single run implemented by RAxML v.8.0.0 (Stamatakis 2014), with a GTR+G model, 2 threads, and 1000 likelihood bootstrap replicates. We also used Bayesian inference to estimate the gene tree with a Markov Chain Monte Carlo search of the posterior probability distribution of tree space implemented by MrBayes (Ronquist and Huelsenbeck 2003; Ronquist *et al.* 2012). Bayesian analysis had two runs of four chains, and 3 million generations, a GTR plus G substitution model, and no partitions. Convergence and mixing were assessed with Tracer v.1.6, and a burn-in of 25% was excluded before estimating the majority rule consensus tree as a summary of the sample of trees from the posterior probability distribution. The most likely tree is presented as output by RAxML, with *D. thyrsiflorum* and *D. cunninghamii* in a sister relationship to the remainder of the *Dendrobium* species included, which is in reasonable agreement with the topology of previously published phylogenies for *Dendrobium* (Burke *et al.* 2008).

Morphological analyses

A total of 139 plants, being a subset of the 281 individuals measured and scored for the purposes of description, from 52 locations throughout the distribution of *D. kingianum* (Table 1) were selected to capture the breadth of morphological and geographical variation expressed by this lineage. The number of plants from each region used in morphological analysis were: Region One: Stroud/Bulahdelah – nine plants; Region Two: Gloucester/Manning – 24 plants; Region Three: Hastings/Comboyne – 25 plants; Region Four: Coffs Harbour/Dorrigo – 32 plants; Region Five: Northern tablelands New South Wales – 15 plants; Region Six: Lamington/Mt. Tamborine – 17 plants; Region Seven: Gympie/Moreton – 9 plants; Region Eight: Carnarvon Gorge area – 8 plants.

Fresh living material was used for all measurements, which were made in the field when complete data were obtainable, otherwise samples were taken by removing a small number of pseudobulbs together with roots from the side of the plant, which were then grown in aged pine bark in raised beds or pots under greenhouse conditions. Height, width and mode of tapering vary to a differing degree in many populations over the distribution range. There is a general trend toward taller canes in the northern part of the range and shorter canes in the southern part, but dwarf forms may occur in all areas. Leaves vary in width, length, and number per cane. Flower count per raceme, and flower size vary among individuals. Flower colour and flower shape also vary, but these were not included in the analysis.

The core dataset comprised nineteen logically independent characters, including 7 vegetative and 12 floral characters: pseudobulb length; pseudobulb base width; pseudobulb apex width; leaves per cane; leaf length; leaf width; number of pseudobulb segments; number of flowers per raceme; peduncle length; flower length; dorsal sepal length; dorsal sepal width; raceme length; lateral sepal length; lateral sepal width; petal length; petal width; mid lobe width; fore lobe width. For each plant, three measurements from representative organs were made, and the mean value calculated. Where it was not possible to obtain three measurements, due to damaged or missing parts, mean values were calculated from two measurements. The lowermost leaf of the pseudobulb was used for all leaf measurements, and a flower of average appearance used for measurement. This core dataset was used for analysis of variance, and principal components analysis. For multidimensional scaling, an expanded dataset with additional metric and nominal variables was used, see details below. The plants were assigned to one of three taxa following the circumscriptions proposed by Clements and Jones (2002), and were scored for their region of origin, regions defined as illustrated in Figure 1.

Table 2. Specimen or reference details and GenBank accession numbers for sequences included in nrITS gene tree. Sequences newly generated for this study are indicated in bold. Vouchers for these specimens are destined for NSW herbarium, their deposition has been hampered by the COVID-19 pandemic.

Species	GenBank accession	Reference
Dendrobium adae	EU430371	Burke et al. (2008)
Dendrobium aemulum	EU430372	Burke et al. (2008)
Dendrobium amboinense	AB894133	Takamiya et al. (2018)
Dendrobium (Grastidium) baileyi	AY240016	Clements (2003)
Dendrobium bifalce	EU430373	Burke et al. (2008)
Dendrobium bigibbum var bigibbum	KP142215	Adams (2015)
Dendrobium bigibbum var bigibbum	KP142214	Adams (2015)
Dendrobium bigibbum var bigibbum	KP142212	Adams (2015)
Dendrobium bigibbum var superbum	KP142211	Adams (2015)
Dendrobium bigibbum var superbum	KP142213	Adams (2015)
Dendrobium callitrophilum	EU430374	Burke et al. (2008)
Dendrobium canaliculatum	EU430375	Burke et al. (2008)
Dendrobium carrii	EU430376	Burke et al. (2008)
Dendrobium (Flickingeria) cognatum	AY240015	Clements (2003)
Dendrobium cunninghamii	AY240019	Clements (2003)
Dendrobium falcorostrum	EU430377	Burke et al. (2008)
Dendrobium finniganense	EU430378	Burke et al. (2008)
Dendrobium fleckeri	EU430380	Burke et al. (2008)
Dendrobium fractiflexum	AY239949	Clements (2003)
Dendrobium furcatopedicellatum	AF521611	Tsai et al. (2004)
Dendrobium gracilicaule	EU430382	Burke et al. (2008)
Dendrobium haemoglossum	HM054638	Singh et al. (2012)
Dendrobium ischnopetalum	AY240007	Clements (2003)
Dendrobium jonesii var. magnificum	EU430383	Burke et al. (2008)
Dendrobium kingianum subsp. kingianum	**MW521085**	Haystack_269
Dendrobium kingianum subsp. kingianum	**MW521086**	Casino_699
Dendrobium kingianum subsp. kingianum	**MW521087**	Gloucester_PA8
Dendrobium kingianum subsp. kingianum	**MW521088**	Coongara_PA11
Dendrobium kingianum subsp. kingianum	**MW521089**	Lamington_PA7
Dendrobium kingianum subsp. kingianum	**MW521090**	Cloud_Ck_PA9
Dendrobium kingianum subsp. kingianum	**MW521091**	Mt_Tavingha_PA10
Dendrobium kingianum subsp. kingianum	**MW521092**	Mt_Alum_PA6
Dendrobium kingianum subsp. carnarvonense	EU430384	Burke et al. (2008)
Dendrobium kingianum subsp. kingianum	EU430386	Burke et al. (2008)
Dendrobium kingianum subsp. kingianum	AB894138	Takamiya et al. (2018)
Dendrobium kingianum subsp. kingianum	KJ672680	Hou, Luo and Ding, unpublished
Dendrobium kingianum subsp. kingianum	AF521075	van den Berg et al. (2005)
Dendrobium kingianum var. pulcherrimum	EU430385	Burke et al. (2008)
Dendrobium linguiforme	AF321593	Perkins and Weston, unpublished
Dendrobium macrophyllum	AY239979	Clements (2003)
Dendrobium macrophyllum	AB894131	Takamiya et al. (2018)
Dendrobium (Cadetia) maidenianum	AY239948	Clements (2003)
Dendrobium moorei	EU430388	Burke et al. (2008)
Dendrobium nindii	AY239985	Clements (2003)
Dendrobium oppositifolium	LC227998	Takamiya et al. (2018)
Dendrobium plicatile	KY966573	Li et al. (2018)

Species	GenBank accession	Reference
Dendrobium pugioniforme	AF321594	Perkins and Weston, unpublished
Dendrobium racemosum	EU430389	Burke et al. (2008)
Dendrobium salaccense	JN388577	Li et al. (2012)
Dendrobium schoeninum	EU430390	Burke et al. (2008)
Dendrobium shiraishii	AB894132	Takamiya et al. (2018)
Dendrobium somae	EU840692	Takamiya et al. (2011)
Dendrobium somae	HM590380	
Dendrobium speciosum	AY239998	Clements (2003)
Dendrobium speciosum	AB894143	Takamiya et al. (2018)
Dendrobium speciosum var. blackdownense	EU430391	Burke et al. (2013)
Dendrobium speciosum var. boreale	KC811539	Burke et al. (2013)
Dendrobium speciosum var. boreale	KC811541	Burke et al. (2013)
Dendrobium speciosum var. boreale	EU430392	Burke et al. (2008)
Dendrobium speciosum var. boreale	KC811542	Burke et al. (2013)
Dendrobium speciosum var. boreale	KC811538	Burke et al. (2013)
Dendrobium speciosum var. boreale	KC811534	Burke et al. (2013)
Dendrobium speciosum var. boreale	KC811531	Burke et al. (2013)
Dendrobium speciosum var. boreale	KC811532	Burke et al. (2013)
Dendrobium speciosum var. capricornicum	KC811545	Burke et al. (2013)
Dendrobium speciosum var. capricornicum	KC811543	Burke et al. (2013)
Dendrobium speciosum var. capricornicum	KC811544	Burke et al. (2013)
Dendrobium speciosum var. capricornicum	EU430393	Burke et al. (2008)
Dendrobium speciosum var. carnarvonense	EU430394	Burke et al. (2013)
Dendrobium speciosum var. curvicaule	KC811533	Burke et al. (2013)
Dendrobium speciosum var. curvicaule	EU430395	Burke et al. (2008)
Dendrobium speciosum var. curvicaule	KC811535	Burke et al. (2013)
Dendrobium speciosum var. grandiflorum	EU430396	Burke et al. (2008)
Dendrobium speciosum var. hillii	EU430397	Burke et al. (2008)
Dendrobium speciosum var. pedunculatum	KC811540	Burke et al. (2013)
Dendrobium speciosum var. pedunculatum	EU430398	Burke et al. (2008)
Dendrobium speciosum var. pedunculatum	KC811536	Burke et al. (2013)
Dendrobium speciosum var. pedunculatum	KC811537	Burke et al. (2013)
Dendrobium speciosum var. speciosum	EU430399	Burke et al. (2008)
Dendrobium taurinum	AB894142	Takamiya et al. (2018)
Dendrobium teretifolium var. fasciculatum	AY240008	Clements (2003)
Dendrobium tetragonum subsp. giganteum	KC811548	Burke et al. (2013)
Dendrobium tetragonum subsp. giganteum	KC811546	Burke et al. (2013)
Dendrobium tetragonum subsp. giganteum	EU430400	Burke et al. (2008)
Dendrobium tetragonum subsp. giganteum	KC811549	Burke et al. (2013)
Dendrobium tetragonum subsp. giganteum	EU430401	Burke et al. (2008)
Dendrobium tetragonum subsp. giganteum	KC811547	Burke et al. (2013)
Dendrobium tetragonum subsp. tetragonum	KC811551	Burke et al. (2013)
Dendrobium tetragonum subsp. tetragonum	KC811552	Burke et al. (2013)
Dendrobium tetragonum subsp. tetragonum	EU430403	Burke et al. (2008)
Dendrobium tetragonum subsp. tetragonum var. melaleucaphilum	EU430402	Burke et al. (2008)
Dendrobium tetragonum subsp. tetragonum var. serpentis	KC811550	Burke et al. (2013)
Dendrobium thyrsiflorum	AY24001	Clements (2003)

The distribution of some variables exhibited right skew, and while parametric multiple analysis of variance (manova) is generally robust to such violations (Olson 1974), we used permutational manova to test the null hypothesis that taxa, and regions, were no more different than expected by chance. All variables were standardised to unit variance by subtracting the variable mean from each observation and dividing by the variable standard deviation; this equalised variate contribution to pairwise distance among individuals, which was calculated using a Euclidean measure of association. Because we were interested in the contribution to overall variance by factors, not just the rank dissimilarities, we performed a permutational multivariate analysis of variance using distance matrices (Anderson 2001), implemented by the adonis function of package vegan 2.5-6 (Dixon 2003). We analysed a design with taxon and region treated as independent factors with an interaction term, and the significance of observed statistics estimated was estimated from 999 permutations to reduce Type 1 error.

Multidimensional Scaling (MDS) provides a means of visually representing the similarities and differences among samples. The same representative sample of 139 plants was analysed. Combined floral and vegetative data were analysed for all regions to determine differences and similarities between plants from different locations and from plants in areas described as different taxa. Morphometric analysis was conducted based on the characters in Table 3 using NTSYS pc Version 2.21. Data for each character were range standardised, such that the range of all characters equalled one unit, giving all characters equal weight. Pairwise distances between specimens were calculated using the Manhattan Metric, and the distance matrix subjected to ordination using non-metric MDS (Kruskal 1964). Ordinations were performed in three dimensions, to give an acceptable level of "stress" in the analysis, i.e. a good level of fit between the visual representation and the original distance matrix (Sneath and Sokal 1973, Milligan and Cooper 1988).

Principal component analysis (PCA) provides an effective means of extracting the main parameters of morphological variation (Dryden and Mardia 1998), by building linear and uncorrelated combinations of morphometric variables to maximise the sample variance explained by the first axis. Remaining axes were orientated orthogonally, with the same aim, and sequentially explain all the remaining variance. Principal components analysis was performed by the prcomp function in stats v.3.5.2 package (R Core Team 2018), again with variables scaled to have unit variance, and Euclidean pairwise distance between individuals, and analyses were conducted in R v.3.5.2 (R Core Team 2018).

Results

Gene tree reconstruction

The 14 *D. kingianum* nrITS sequences belonged to 11 haplotypes, due to differences at 14 variable sites, involving G-C, G-A, and C-T substitutions; 4 deletions of 1 or 2 bases, and an insertion of variable length involving a GA tandem repeat, which was longest in the individual from Cloudy Creek.

In the Bayesian analyses of nrITS sequences, the tree likelihood, base frequencies, and substitution matrix parameters all had effective sample sizes greater than 600 in the single runs, and marginal probability distributions overlapped with shared peaks, suggesting stationarity and convergence in the replicate searches.

In both the most likely tree and the Bayesian Majority Rule (MJ Rule) tree the individuals of *Dendrobium kingianum* group within a strongly supported lineage, but the species was rendered paraphyletic by *D. moorei* (Fig. 2). However, this paraphyly was not supported. Aside from *D. kingianum* subsp. *carnarvonense,* the other samples of *D. kingianum* formed two strongly supported monophyla, one containing individuals from the southern part of the distribution from Casino south, the other containing plants from northern part of the range from Dorrigo (Cloudy Creek) north. Three individuals of *D. kingianum* var. *pulcherrimum* formed a supported monophylum within the southern lineage.

Dendrobium kingianum was resolved sister to *D. speciosum* with strong support, as reported by Burke *et al* (2008). The monophyly of *D. speciosum* was unsupported, in contrast to the full support for the three nrITS lineages resolved within that species. Northern varieties including *D. speciosum* var. *curvicaule*, *D. speciosum* var. *boreale,* and *D. speciosum* var. *pedunculatum* were resolved among two lineages, and the southern lineages were resolved in a monophylum sister to the northern lineage containing the sampled individuals of *D. speciosum* var. *curvicaule.*

Table 3. Morphological characters used in morphological analyses.

Vegetative Characters
Pseudobulb length (cm)
Pseudobulb width at base (cm)
Pseudobulb width at midpoint (cm)
Pseudobulb width at top (cm)
Number of segments along pseudobulb
Collum[A] 0/0.25/0.5/0.75/1.0 0= absent 1= strongly present
Number of leaves
Leaf length (cm)
Leaf width (cm)
Leaf thickness (mm)
Aerial roots [A] 0/1/2/3/4 0 = absent 4 = strongly present
Pseudobulb – midpoint width/base width
Floral Characters
Number of flowers per inflorescence
Rachis length (cm)
Peduncle length (cm)
Peduncle width (mm)
Flower length (dorsal sepal tip – lateral sepal tips) (cm)
Flower length (dorsal sepal tip – mentum) (cm)
Flower width across petals (as presented) (cm)
Flower width across petals (flattened) (cm)
Flower width at mentum (as presented) (cm)
Flower width at mentum (flattened) (cm)
Dorsal sepal length (cm)
Dorsal sepal width at base (cm)
Petal length (cm)
Petal width at base (mm)
Petal width at widest point (mm)
Individual lateral sepal width at base (cm)
Width of lateral sepals at widest point (as presented) (cm)
Width of lateral sepals at widest point (flattened) (cm)
Distance between lateral sepal tips (as presented) (cm)
Distance between lateral sepal tips (flattened) (cm)
Inner width of lateral sepals at widest point (flattened) (cm)
Pedicel length (cm)
Ovary length (cm)
Flower stalk length (cm)
Labellum length (cm)
Midlobe length (cm)
Midlobe width (cm)
Forelobe length (cm)
Forelobe width (cm)
Forelobe presentation width (mm)
Dorsal sepal length:width
Dorsal sepal length:labellum length
Flower length:labellum length ratio
Peduncle length:rachis length
Labellum length:midlobe length

[A] denotes nominal character

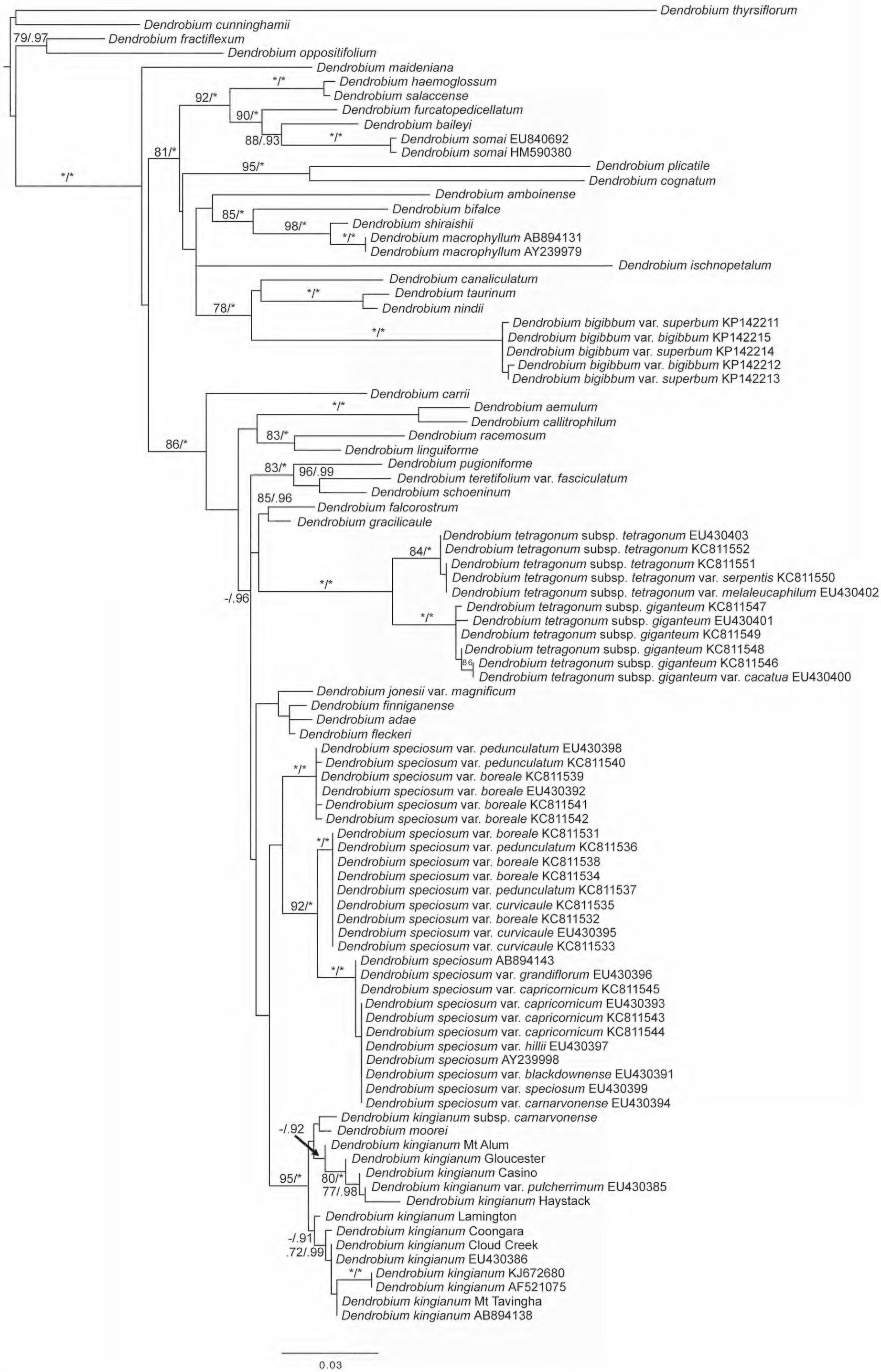

Figure 2. The most likely tree estimated for the nrITS sequences. Numbers associated with branches show likelihood bootstrap and posterior probability values, the latter from Bayesian analysis of the same dataset, respectively with * representing full support (100% and 1.0).

Morphological Analysis – Multidimensional Scaling

All plants ordinate within the space occupied by *D. kingianum* subsp. *kingianum*, with no isolated subgroups (Fig. 3). Plants ascribed to *D. kingianum* var. *pulcherrimum sensu* Rupp, being three plants from northern NSW and eight plants from the three southernmost regions of the distribution, occupy a broad central area of the ordination space, admixed with *D. kingianum* subsp. *kingianum*. Plants described as *D. kingianum* subsp. *carnarvonense* group towards one side of the ordination space. Some ordinate with tall straggly plants with narrow leaves from the northern and western limits of distribution where conditions are more extreme, for example the coastal southern Queensland area (Region 7).

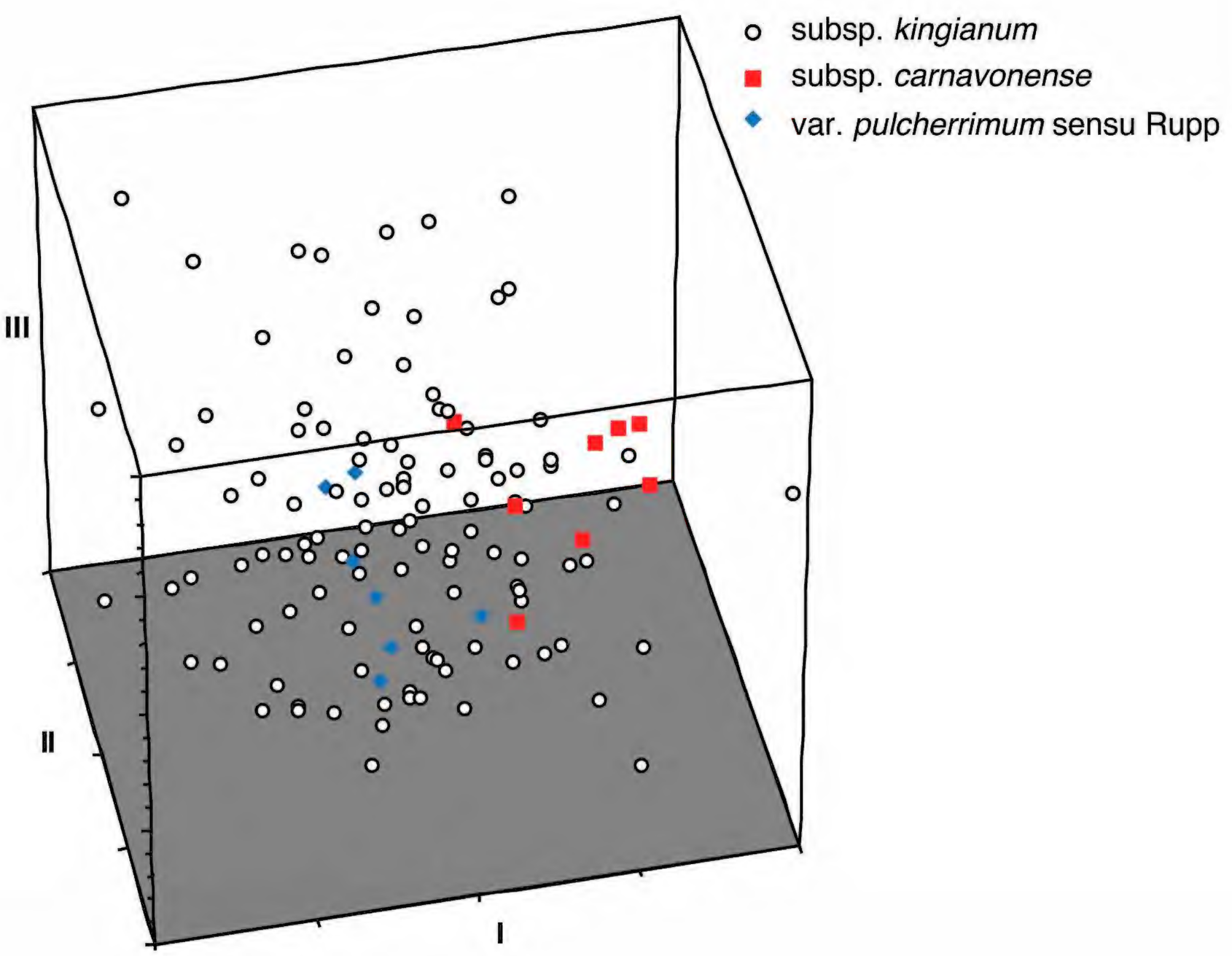

Figure 3. Ordination summarising variation among individuals in 19 morphological characters, summarising variation among individuals belonging to three commonly recognised taxa.

Plants of all regions overlap. Region 8 plants ordinate in the same space as some plants from regions 5, 6 and 7. Taller plants tend to ordinate towards one end of the space, and shorter ones at the other, with much overlap. Shorter plants from regions 1, 2 and 4 that correspond to *Dendrobium kingianum* var. *pulcherrimum* are mixed within the larger group.

Morphological analysis - Principal Components Analysis

Dendrobium kingianum subsp. *kingianum, D. kingianum* var. *pulcherrimum* and *D. kingianum* subsp. *carnarvonense* all have different centroids in multivariate morphological space (Fig. 4). Just over 9% of variation contributed by differences among taxa. Centroids are also significantly different among regions, which contributed 28% of residual sums of squares (Table 4). There was no significant interaction between putative taxon and region, implying the putative taxa are not geographically segregated. The first principal component (PC) explained 33% of variation among individuals. Characters with highest loading on the first PC were all associated with flower size, suggesting this axis broadly summarises differences in flower size among individuals (Table 5). *Dendrobium kingianum* subsp. *carnarvonense*, to which individuals from region 8 belong, are the only plants that separate along this axis, forming a distinct but not discrete cluster at the negative end (Fig. 4a). *Dendrobium kingianum* subsp. *carnarvonense* overlap with some individuals of *D. kingianum* subsp. *kingianum* from regions 4, 5, and 7. The distribution of individuals along PC1 suggests wide variation in flower size is a feature of most regions, with the largest flowers being found in regions 2, 3, and 6.

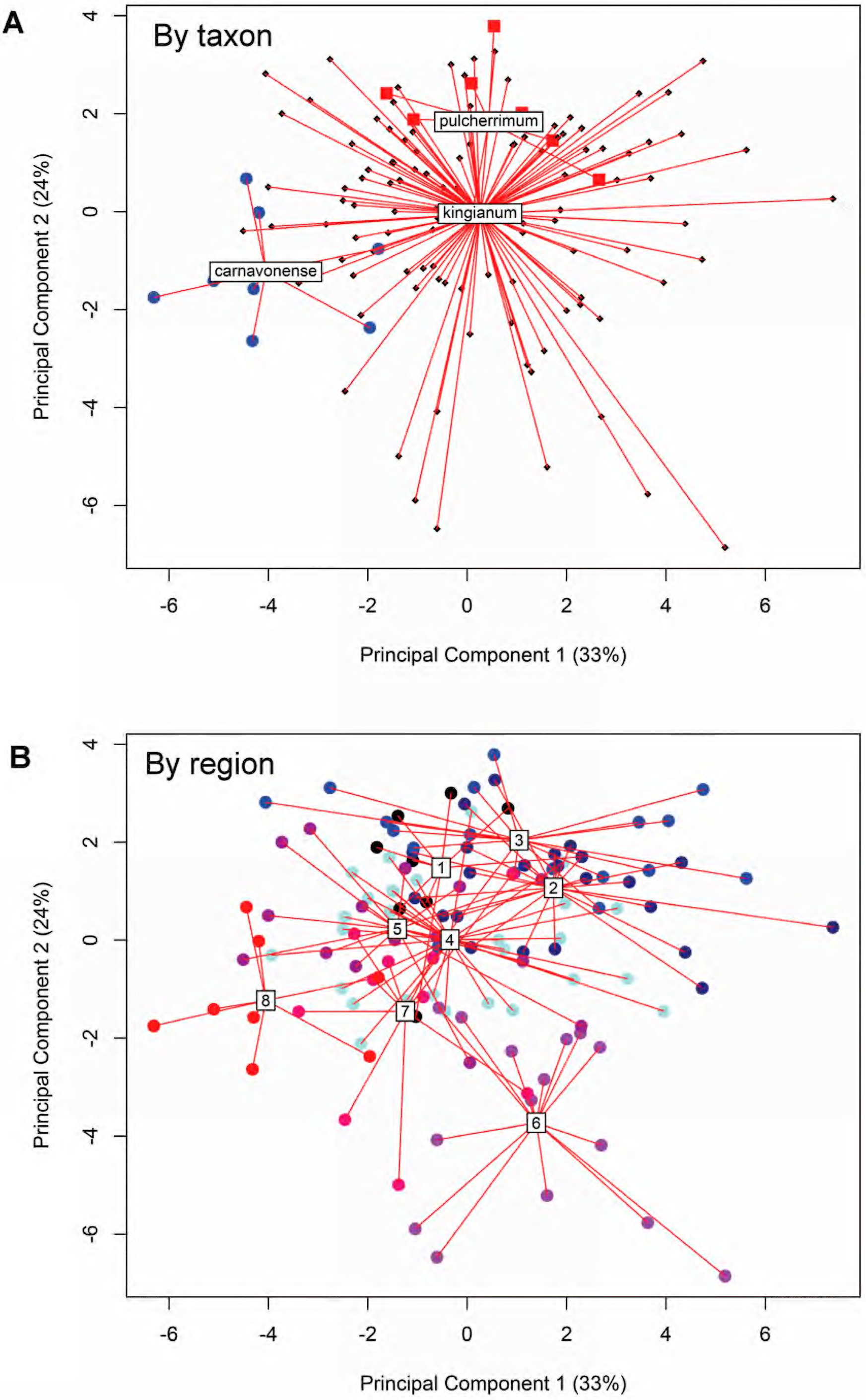

Figure 4. Principal components plot summarising variation among individuals in 19 morphological characters, showing centroids and distribution of individuals belonging to (A) three commonly recognised taxa; and (B) the eight regions in which *D. kingianum* occurs.

Table 4. Summary statistics from permutational MANOVA of morphological data.

	Df	SumsOfSqs	MeanSqs	F.Model	R^2	Pr(>F)	
Taxa	2	220.24	110.120	8.6195	0.09127	0.001	***
Region	6	676.66	112.776	8.8274	0.28042	0.001	***
Taxa : Region	2	21.35	10.675	0.8355	0.00885	0.573	
Residuals	117	1494.75	12.776		0.61946		
Total	127	2413.00			1.00000		

Table 5. Character loadings on principal components analysis.

	PC1	PC2	PC3	PC4	PC5
pseudobulb length	0.0726	-0.3931	0.0027	-0.2367	0.0611
pseudobulb base	0.1737	-0.0614	-0.5153	0.1055	0.2286
pseudobulb apex width	0.1944	-0.0704	-0.5350	0.1533	0.0824
leaves per cane	0.0122	-0.3628	-0.0737	-0.0571	-0.3961
leaf length	0.0494	-0.3619	0.0682	-0.0173	0.2296
leaf width	0.1657	-0.3423	-0.1854	-0.1334	-0.1688
number of pseudobulb segments	-0.0342	-0.3876	0.0842	-0.3772	0.0122
number of flowers per raceme	0.1850	-0.2714	0.0521	0.1997	-0.4692
peduncle length	0.1220	-0.2438	0.1676	0.4954	0.3781
flower length	0.3048	0.0145	0.2064	-0.1803	0.2484
doral sepal length	0.3027	0.0621	0.2918	-0.0359	0.0298
dorsal sepal width	0.2648	0.0264	-0.1923	-0.3165	0.1492
raceme length	0.2284	-0.2508	0.1703	0.3895	0.1539
lateral sepal length	0.3311	0.0987	0.1781	0.0110	-0.2537
lateral sepal width	0.2408	0.1617	-0.1270	0.3136	-0.3865
petal length	0.3267	0.0836	0.2431	-0.0079	0.0428
petal width	0.2882	0.1772	-0.2418	-0.0695	0.0882
midlobe width	0.3120	0.1194	0.0781	-0.1791	-0.0623
forelobe width	0.2912	0.1321	-0.0254	-0.1979	0.0002

The second PC explained 24% of variation among individuals. Characters with high loading on this axis were predominantly associated with pseudobulb and leaf size, but also the number of flowers per raceme and the peduncle length, which are all positively correlated with one another, and negatively correlated with PC2. Plants of *D. kingianum* var. *pulcherrimum* cluster toward the positive end of PC2, but they do not fall beyond the range of *D. kingianum* subsp. *kingianum*, whose individuals are more or less continuously distributed along this axis (Fig. 4A). Some separation among regions was achieved along PC2, plants from southern regions 1, 2 and 3 have centroids closest to the positive end of the axis, while plants from south-east Queensland and far north-east New South Wales have their centroid closest to the negative end (Fig. 4B). Individuals from region 7, and regions 1, 2, and 3 occupy non-overlapping subsets of multivariate morphological space, due to differences in vegetative morphology, flower count, and flower peduncle length.

Discussion

The nuclear ITS gene tree resolved *D. kingianum* paraphyletic with respect to *D. moorei*, but with no positive support for this topology, because the relationships of *D. moorei* within the *D. kingianum* clade are unsupported. Splits networks from AFLP data have also recovered a close relationship between *D. kingianum* and *D. moorei,* but resolved a single cluster corresponding with *D. kingianum* (Simpson *et al.* 2018). More nrITS haplotypes were detected among a smaller number of individuals of *D. kingianum* than within *D. speciosum*, suggesting *D. kingianum* may contain relatively higher levels of haplotype diversity in this marker, which may indicate lower effective gene flow among populations of the latter species. Where the sample of 26 individuals of *Dendrobium speciosum* yielded 7 haplotypes separated by 1–3 base differences and short indels, the sample of 14 *D. kingianum* returned 11 nrITS haplotypes. These 11 haplotypes exhibit a geographic pattern of relationships suggesting that geographic partitioning may contribute to the high haplotype diversity within *D. kingianum*.

Dendrobium kingianum is an inhabitant of rock outcrops, rock pavements, boulder fields, bluffs, cliff lines, gullies, gorges and ravines, and occurs as a mosaic of populations within the Australian landscape as a function of the existence of suitable habitat. Orchid populations may supply the majority of their own recruits, and gene

flow among populations by pollen and seed transport may be limited, despite the apparent dispersability of small dust-like orchid seeds (Kotilínek *et al.* 2020). The lack of genetic panmixis that results from populations inhabiting relatively isolated habitat patches may contribute to the accumulation of regional differences in haplotype diversity, as known in other rainforest taxa (Heslewood *et al.* 2014). This regionalisation could be promoted by fluctuation in population sizes, such that shared ancestral haplotypes were purged from populations by stochastic processes during periods of small effective population size, as might result from glacial-interglacial cycling. Environmental niche modelling for the southern lineage of *Dendrobium speciosum* has predicted contraction of core habitat during the last glacial maximum (Simpson *et al.* 2018), consistent with the contraction of other species associated with rainforest habitats (Das *et al.* 2019). *Dendrobium kingianum* may exhibit a similar response. During glacial interglacial climate cycling through the Quaternary, rainforests have repeatedly contracted to core refugia (Van Der Waal *et al.* 2009) and have expanded in range and extent of occurrence since the last glacial maximum (Fahey *et al.* 2019; Whitehead *et al.* 2019). The results from the nrITS gene tree are suggestive, but the geographically structured genetic diversity may have a climatic component. The geographic distribution of genetic diversity within *D. kingianum* warrants further investigation, particularly with respect to establishing the dynamics of recruitment, and the potential existence and distribution of refugia.

In turn, there is a strong geographic component to the partitioning of morphological variation. During periods of climatic stress and small population size, selection may promote adaptive morphological divergence, as may have been the case at the southern end of the distribution, and indeed at higher elevations where short stature, clump-forming morphotypes predominate. These morphotypes may be adaptive in water-limited or cold environments. Studies from bryophytes demonstrate reduced water loss associated with clump forming habit due to reduced surface area to volume ratio, and activation of a boundary-layer effect that slows evaporation (Sand-Jensen and Hammer 2012; Zotz *et al.* 2000). Clumping may also facilitate warming, and slow the rate of cooling after dark, which may be especially important if *Dendrobium kingianum* is a C_4 plant. Cushion-forming alpine plants are known to warm at the same rate as the air, but cool at a slower rate than air (Sklenar *et al.* 2016). Both rates may be important at the southern end of *D. kingianum*'s distribution during periods of historical climate-induced stress, as may have occurred during glacial maxima. Conversely, we may be witnessing a peak in the extent and abundance of *D. kingianum* distribution, where the species currently occupies most of the suitable sites throughout its range, in which context many of the previously effective distance-based barriers to gene flow have been reduced or removed.

At the northern end of *D. kingianum* distribution we see a pattern that may be different from that observed at the south – a population currently confined to a mesic refugium within a canyon system. The climate currently constraining the distribution of *D. kingianum* in Carnarvon Gorge may be the result of longer-term cooling and drying of the Australian continent (Martin 2006). Today, conditions at the north-western limits of *D. kingianum* distribution may be promoting the unusual subterranean growth habit of *D. kingianum* subsp. *carnarvonense*, as the population shelters from climatic extremes by growing partially underground. Interactions with climate at two very different temporal and spatial scales, one a continent scale cooling and drying that has occurred millions of years, the other glacial-interglacial cycling that occurs over tens of thousands of years and likely has more pronounced impacts in the south of Australia, may contribute to the morphological diversity seen in contemporary *D. kingianum* populations.

Individuals from the southern end of *D. kingianum*'s distribution look different vegetatively from individuals in the coastal districts at the northern end of the distribution, although there are no qualitative character differences. A number of quantitative character differences could be used to circumscribe the morphotypes most frequent in each region, and these could be considered for recognition as different taxa. However, the proposition of species status for plants from different regions would overlook two critical factors integral to the utility of species. The first is that explaining a difference in morphology among individuals by the existence of different species neglects a hierarchy of variance components that may also explain those differences among individuals. The second is the broader geographic and climatic context that has resulted in those patterns. Species often preserve a signature of dynamic interaction with their environmental and ecological context, from which we can infer aspects of species history and life history (Rossetto *et al.* 2008; Rutherford *et al.* 2018; Whitehead *et al.* 2019). That signature often manifests in the form of intra-specific morphological variation.

Data from field observations of variation over the whole distribution range support a single species with wide variability of plant form and flowers. Two morphological and geographic sub-groups can be recognised. These have been formalised as subspecies which are now widely accepted (WCSPF 2018). Within the typical subspecies, morphological variation is more or less continuous, and exhibits a strong signature of regionalisation, at the same time as regions exhibit overlap and continuity in their parameters of morphological variation. Short, very clumped plants with small flowers represent one end of a continuum in morphological variation at the southern end of the distribution. Plants with relatively large flowers fitting the description of *D. kingianum* var. *pulcherrimum*

Rupp are scattered and very occasional over the southern half of the range. The geographic partitioning of a continuous spectrum of clinal variation, and nestedness of individuals of *D. kingianum* var. *pulcherrimum* within *D. kingianum* in the nrITS gene tree, both support the interpretation that individuals with the *D. kingianum* var. *pulcherrimum* morphotype are one expression of a variable *D. kingianum* subsp. *kingianum.*

Morphological data from PCoA and MDS support recognition of a single morphologically variable species, with a morphologically distinct subspecies in the north-west (Figures 3, 4). These results are compatible with the occurrence and distribution of molecular diversity recovered by this and previous studies of variable section *Dendrocoryne* species such as *Dendrobium speciosum* (Burke *et al.*, 2008, Simpson *et al.* 2018). No subgroups that could provide support for separate species within *D. kingianum* could be found in either the molecular or morphological data sets. The diminutive midlobe and partially subterranean habit of *D. kingianum* subsp. *carnarvonense*, together with the disjunct distribution supports the circumscription of the subspecies as initially described by Adams (Adams and Lawson 1995), in addition to the characters included in the morphological analysis completed here. Subspecies is appropriate for the Carnarvon Gorge plants because of their disjunct distribution, membership of a broader lineage corresponding with *D. kingianum,* and broad morphological overlap with *D. kingianum* subsp. *kingianum*. However, there are some plants at the western distribution limit of *D. kingianum* subsp. *kingianum* that may exhibit a similar degree of subterranean habit, as in typical *D. kingianum* subsp. *carnarvonense*. Unlike many orchid species, the labellum shape varies considerably in *D. kingianum*, in most regions and even in a single population (Table 6), and is not useful in circumscribing intra-specific taxa.

Table 6. Variation in Flower Colour and Midlobe Types in a population of *Dendrobium kingianum* at Gloucester, New South Wales

Plant No.	Flower Colour	Midlobe Type	Midlobe Point*
1.	purple	spade	-
2.	midmauve	oval	+
3.	midmauve	broadheart	+
4.	pale mauve	spade and pointed spade	+/-
5.	midmauve	oval and spade	-
6.	midmauve	oval	-
7.	midmauve	broadheart	+
8.	deep mauve	broadheart	+
9.	pale mauve	broadheart	+
10.	midmauve	spade	-
11.	splash purple	broadheart	+
12.	pale mauve	pointed spade	
13.	pale mauve	broadheart	+
14.	splash mauve	broadheart	+
15.	midmauve	oval and spade	+/-
16.	midmauve	large globular	+
17.	pale mauve	broadheart	+

*

+ midlobe point present

- midlobe point absent or diminutive

Field studies coupled with analyses of morphological and molecular variation allow consideration of the status of all previously proposed taxa informed by morphological and molecular data. Firstly, this study of the whole distribution revealed no evidence to support the proposed segregate taxa of Clements and Jones (2002) with variation being continuous and best explained by a single species. Secondly, the historic varieties *Dendrobium kingianum* var. *aldersoniae*, *D. kingianum* var. *pallidum*, *D. kingianum* var. *pulcherrimum* and *D. kingianum* var. *silcockii* are all retained in synonymy with *D. kingianum* subsp. *kingianum* as recommended by Adams and Lawson (1995), as these varieties all represent colour and growth forms of a single variable species (Fig. 5).

Figure 5. A representative range of flowering individuals of *Dendrobium kingianum* from each region, illustrating diversity in vegetative and floral form expressed by this morphologically variable species; (A) Region 1. Mt. Alum. (B) Region 2. Gloucester (a triploid). (C) Region 3. Haystack (*D. kingianum* var. *pulcherriumum* Rupp). (D) Region 3. Stony Creek. (F) Region 4. Cloud Creek (*D. kingianum* var. *silcockii* F.M.Bail.).(E) Region 3. (*D. kingianum* var. *pulcherriumum* Rupp). (G) Region 6. Busby's Flat. (H) Region 6. Tarlington. (I) Region 7. Mt. Timbeerwah. (J) Region 8. Robinson Gorge (*D. kingianum* subsp. *carnarvonense*).

Taxonomic treatment

Dendrobium kingianum Bidwill ex Lindl. *Edwards' Botanical Register* 30: misc. 11 (1844)

Original material: 'This curious plant was bought by the Messers. Loddiges at the sale of Mr Bidwill's New Holland Plants'

Type: K 001089618 *fide* Clements (1989)

Callista kingiana (Bidwill ex Lindl.) Kuntze. *Revis. Gen*. pl. 2:654 (1891)

Dendrocoryne kingiana (Bidwill ex Lindl.) Brieger, in Schlechter *Die Orchideen* Ed. 3 (11/12): 724 (1981)

Tropilis kingiana (Bidwill ex Lindl.) Butzin, *Willdenowia* 12(2): 250 (1982)

Tropilis kingiana (Bidwill ex Lindl.) Rauschert, *Feddes Repert*. 94(78): 470 (1983) *nom. superfl.*

Thelychiton kingianus (Bidwill ex Lindl.) M.A.Clem. & D.L.Jones *The Orchadian* 13(11): 491 (2002)

General description based on all geographic regions

Plants growing together and forming large congested clumps or growing as separate individuals, of widely variable habit from miniature, short compact forms to medium and tall, upright urn shapes or spreading, scrambling plants with horizontal and downward arching pseudobulbs. Aerial growths absent, occasional or common, especially on older and leafless pseudobulbs. Pseudobulbs very variable, from very short (4 cm) to long (30 cm, rarely to 60 cm), broadest (up to 2.5 cm) at the base and tapering upwards to a narrow apex (0.25–0.7 cm), segments 2–7, most commonly 3–5; when young, covered or partly covered with thin brown or green papery bracts which disintegrate with age to reveal a green, brown or purple surface with longitudinal grooves. Leaves apical, 2–7 per pseudobulb, most commonly 3 or 4, narrow, elliptical to ovate, 3.5–12 cm long, 1.1–3.9 cm wide. Colour usually mid green or grey green with or without red purple tints, the tints pronounced when plants are exposed to strong light. There is a tendency in some plants towards very narrow leaves produced in a single plane, or variably twisted about the long axis. Plants variably floriferous, either one raceme per pseudobulb or multi-racemed pseudobulbs with dense floral displays. Floral racemes 1–3, green to deep purple in colour, arising terminally from the pseudobulbs and occasionally from a variable number of lateral nodes between and below the origin of the leaves, racemes erect to semipendulous; peduncle variable from 3.5–14.5 cm long, inflorescence 8–22 cm long.. One to fifteen flowers per raceme, on pedicels 1.0–1.5 cm long. Flower colour variable even within small populations, from pure white to solid purple, tending most commonly to splash purple and pale to mid mauve with a mid to deep purple speckled labellum. Occasionally the labellum is almost solid purple, rarely it is pure white. Flowers presenting cupped to planar, more commonly cupped and of medium substance (firmness of the plant tissue), occasionally with a deeper colour on the reverse side (northern plants). The mentum may be tinged with pale green or mauve-purple. Dorsal sepal keel 1.3–3.0 cm long, dorsal sepal 1.0–2.2 cm long, 0.3–0.8 cm wide, lateral sepals spanning 2.2–4.1 cm, 0.9–1.7 cm wide, petals 0.9–1.0 cm long, 0.2–0.7 cm wide. Floral segments from acute to rounded. Labellum c.1.6 cm long, 1.0 cm wide, curved, variously striped or speckled with pale mauve to deep purple, or white; three lobed, very narrow at the base, lateral lobes narrow, usually erect or curved, and column embracing but occasionally flared outwards away from the column. Midlobe shape variable, sometimes two or three distinct shapes on the same plant, including oval, pointed spade, spade, bilobed spade, narrow-cordate, broadly cordate and occasionally rotund (similar to Table 6). Midlobe presentation width (diameter of midlobe in naturally presented flowers) 0.6–1.1 cm, forelobe presentation width (distance between lateral lobes in naturally presented flowers) 0.4–0.85 cm. Callus on lamina green, yellow, colourless or white, with three low or distinctly elevated ridges, often conspicuously divided into three lobes at the anterior end. Apex of midlobe pointed or point absent, angled variously, often recurved. Column c. 0.4 long by 0.3 cm wide, dilated laterally at the midportion and curved or angled sharply to an almost straight foot 0.5–0.9 cm long. Anther ovoid to subreniform viewed from above, pollinia slender, subequal, and falcate-obovoid. Nectary at base of column foot, varying from yellow to green in colour, most commonly green.

Representative specimens examined are listed in Table 7 and lodged at MELU and NSW.

Table 7. *Dendrobium kingianum* specimens lodged at Herbaria

Name	Collection No.	Region	Herbarium	DNA sampled
subsp. *kingianum*				
Mt. Alum	1088	1	NSW	+
Mt. Alum	1188	1	NSW	-
Main Creek Dungog	861	1	NSW	-
Waukivory Pink	865	2	NSW	-
Gloucester Shell Pink	1867	2	NSW	-
Rowleys Ridge	893		NSW	-*
Ha Ha (No. 21)	1922/549	2	NSW	+
AF22	669	2	NSW	-
Gloucester Red No.1	290	2	NSW	-
Gloucester Red No.2	563	2	NSW	-
Haystack	490	3	NSW	+ *
Mt. Boss	1282	3	NSW	-
Tunstead's Pink	426	3	NSW	-
Lansdowne	850	3	NSW	-
Stony Creek	167	3	NSW	-
Yarras White	1281/1196	3	NSW	-
Port Macquarie	136	3	MELU	EU430385
Dorrigo Red	1421	4	NSW	-
Len Archer Pulcherrimum	699	4	NSW	+*
Cloud Creek Dorrigo	889	4		+
Keith Preston	288	4	NSW	-
Lipstick	296	4	NSW	-
Gibraltar Range Rock Top	1626	4	NSW	-
Walkerie Rock Pulcherrimum	1983	4	NSW	-
Coledale Morgans Camp	1634/?1636	4	NSW	-
Gibraltar Range R&R	10	5	NSW	-
Boonoo Boonoo Falls	1644	5		-
Boonoo Boonoo	1632	5	NSW	-
Boonoo Boonoo	1605	5	NSW	-
Rocky River 1.	1029	5	NSW	-
Rocky River 2.	1022	5	NSW	-
Busby's Flat White	449	6	MELU	EU430386
Tarlington	640	6	NSW	-
Tarlington	642	6	NSW	-
Lamington Plateau	216	6	NSW	+ ?MELU
Wine Creek	514	6	NSW	-
Busby's Flat Pink Stars	509		NSW	-
Pikapene White	740	6	NSW	-
Corrigan's Red	240	6	NSW	-
Mothar Mountain	926	7	NSW	-
Coongara	268	7	NSW	+?MELU
Tavinghi	1967	7	NSW	+ PA10
Tibrogargan or Timberwah	?961	7	NSW	-
Yangan Toowoomba	896	7	NSW	-
Yangan Toowoomba	917	7	NSW	-
subsp. *carnarvonense*				
Robinson Gorge	1981	8	NSW	-
Carnarvon Gorge	1982	8	NSW	+?MELU
Carnarvon Gorge	1983	8	NSW	-

*pulcherrimum

Key to subspecies

1a. Plants erect to spreading, but not consistently partially subterranean, flowers variable in colour, midlobe greater than 0.6 cm in width with a callus on the labellum bearing conspicuous keels ending in three prominences anteriorly. Plants of southern Queensland and New South Wales..... *D. kingianum* subsp. *kingianum*

1b. Plants consistently partially subterranean, pseudobulbs forming an underground mat with narrow emergent upper portions, leaves long 8.2–13.5 cm and narrow 0.85–1.9 cm, flowers white to pale mauve with very small purple-streaked midlobe, midlobe diameter 0.4–0.5 cm, low callus on labellum with no bluntly-ending anterior keels. Plants of Central Queensland sandstone country .....*D. kingianum* subsp. *carnarvonense*

Dendrobium kingianum* subsp. *kingianum

=*Dendrobium kingianum* var. *album* B.S.Williams, *The Orchid Album* 7: 332 (1887)

Original material: 'For the opportunity of figuring this rare plant we are indebted to A.H. Smee, Esq., The Grange, Carshalton, in whose well-known collection it bloomed in the early part of the present year.'

=*Dendrobium kingianum* var. *pallidum* F.M.Bailey, *The Brisbane Courier* 38(8000): 7 (1883)

Original material: 'Hab. on rocks Main Range, collected by B. Crow and C.H. Hartmann'

Type: Main Range, *B. Crow and C.H. Hartmann* (BRI-AQ0025296, K)

=*Dendrobium kingianum* subvar. *pallidum* J.H.Veitch, *A Manual of Orchidaceous Plants* 1(3): 52 (1887)

Original material: (none cited)

Type: not located

=*Dendrobium kingianum* var. *silcockii* F.M.Bailey, *The Queensland Flora* 5: 1528 (1902)

Original material: 'Found towards the Tweed River, 24th Sept. 1901. P. Silcock.'

Type: Collected from towards the Tweed River, Sept 24th 1901, *P. Silcock* (BRI-AQ0025295; K).

=*Dendrobium kingianum* var. *aldersoniae* F.M.Bailey, *The Queensland Agricultural Journal* 15: 781 (1905).

Original material: Blackall Range, Mrs G. W. Alderson

Type: not located

Dendrobium kingianum var. *aldersonae* F.M.Bailey, *orth. var.*

=*Dendrobium kingianum* var. *pulcherrimum* Rupp, *Orchids of New South Wales*: 116 (1943)

Thelychiton pulcherrimus (Rupp) M.A.Clem. & D.L.Jones, *The Orchadian* 13(11): 492 (2002)

Original material: In Herb. Rupp: Northbridge (cult. plant from the Upper Hastings River, Fieldsend 1937), Rupp 9.1943, Holotype.

Type: Cult. Northbridge, N.S.W. 9. 1943 (HMRR). Plant originally from the Upper Hastings River, N.S.W. (coll. F. Fieldsend) (holotype: NSW 87427!).

Queensland and Border Ranges forms

Description: Plants of variable habit, generally tall, upright, urn shaped with open structure in exposed areas, and scrambling cascades on shaded creek sides. Aerial growths common on most plants. Pseudobulbs usually robust and tending to a vertical orientation with an expanded basal third anchored to rocks in leaf litter or grass; short (10 cm) to long (27 cm), an occasional plant to 60 cm, broadest (up to 2.5 cm) at the base and tapering upwards to a broad apex (0.3–0.7 cm), segments 5–10, most commonly 6–7; when young, covered or partly covered with thin brown or green papery bracts which disintegrate with age to reveal a brown or purple surface with longitudinal grooves. Leaves apical, 3–7 per pseudobulb, most commonly 4–6, narrow, elliptical to ovate, 6.2–12 cm long, 1.8–3.9 cm wide. Colour usually mid green with or without red purple tints, the tints pronounced when plants are exposed to strong light. Plants variably floriferous, including multi-racemed pseudobulbs with dense floral displays. Floral racemes 1–3, arising terminally from the pseudobulbs and occasionally from lateral nodes between and below the origin of the leaves, racemes erect, semierect or pendulous; bearing 3–15 flowers per raceme, commonly 8–10, on pedicels 1–1.5 cm long. Peduncle variable from 5–12 cm long, rachis 7–13 cm, inflorescence 11–22 cm long. Flower colours pure white to solid purple, tending most commonly to splash purple and pale to mid-mauve with a mid to deep purple speckled

labellum. Occasionally the labellum is almost white or solid purple. Flowers presenting cupped to planar, more commonly cupped and of medium to heavy substance, commonly with a deeper colour or strong purple lines on the reverse side. The mentum may be tinged with pale green or mauve purple. Dorsal sepal 1.2–1.7 cm long, 0.55–0.75 cm wide, keel 1.6–2.6 cm long, lateral sepals spanning 2.4–3.4 cm, 1.0–1.3 cm wide, petals 1.0–1.6 cm long, 0.3–0.55 cm wide. Floral segments are usually acute. Labellum approximately 1.5 cm long, 1.0 cm wide, curved, variously striped or speckled with pale mauve to deep purple; three lobed, very narrow at the base, lateral lobes narrow, usually erect, and column embracing. Midlobe shape widely variable, occasionally two or three distinct shapes on the same plant, including oval, pointed spade, spade, broad heart and occasionally globular or narrow heart (similar to Table 6). Midlobe presentation 0.6–0.95 cm wide, forelobe presentation 0.4–0.65 cm wide. Laminar callus green, yellow or colourless to white, with three low to distinctly elevated ridges, often conspicuously divided into three prominent lobes at the anterior end. Apex of midlobe pointed or point absent, angled variously, often recurved. Column generally c. 0.4 cm long, 0.3 cm wide, dilated laterally at the midportion and curved or angled sharply to an almost straight foot 0.5–0.9 cm long. Anther ovoid to subreniform viewed from above, pollinia slender, subequal, and falcate-obovoid. Nectary at base of column foot, from yellow to green in colour, usually green.

Distinctive aspects: In general, there is a trend towards aerialization and longer upright pseudobulbs and raceme habit. Flowers have medium to heavy substance and pointed segments, imparting a starry appearance.

Notes: Characteristics intergrade with those of plants on the Great Dividing Range through the Border Ranges (Queensland, New South Wales) to Gibraltar Range and the Dorrigo region (New South Wales).

Chromosome number: All plants tested were diploid (2n=38) (Adams 1992).

Dorrigo and Gibraltar Range forms

Description: Plants growing together and forming large clumps or growing as separate individuals, of widely variable habit from tall upright urn shape to spreading, scrambling plants with horizontal and downward arching pseudobulbs. Aerial growths are common, especially on older and leafless pseudobulbs. Pseudobulbs variable, from short (7 cm) to long (20 cm), broadest (up to 1.5 cm) at the base and tapering upwards to a narrow apex (0.25–0.4 cm), segments 4–5, most commonly 4; when young, covered or partly covered with thin brown or green papery bracts which disintegrate with age to reveal a green, brown or purple surface with longitudinal grooves. Leaves apical, 3–5 per pseudobulb, most commonly 3 or 4, narrow, elliptical to ovate, 4.5–9 cm long, 1.4–2.1 cm wide. Colour usually mid green with or without red purple tints, the tints pronounced when plants are exposed to strong light. In some plants there is a tendency towards very narrow leaves produced in a single plane, or variably twisted about the long axis. Plants variably floriferous, including multi-racemed pseudobulbs with dense floral displays. Floral racemes 1 or 2, occasionally 3, arising terminally from each pseudobulb and occasionally from lateral nodes between and below the origin of the leaves, racemes erect to semierect; bearing 3–10 flowers per raceme, median 6, on pedicels 1.0–1.5 cm long. Peduncle variable 5–14.5 cm long, rachis 4–9 cm long, inflorescence 9.5–20 cm long. Flower colour pure white to solid purple, or splashed with purple and pale to mid-mauve with a mid to deep purple speckled labellum, occasionally with a deeper colour on the reverse side; the labellum may be almost solid purple. Flowers presenting cupped to planar, more commonly planar and of light to medium substance. The mentum may be tinged with pale green or mauve purple. Dorsal sepal 1.3–1.8 cm long, 0.5–0.6 cm wide, keel 2.1–2.8 cm long, lateral sepals spanning 2.5–3.3 cm, 1.1–1.2 cm wide, petals 1.2–1.7 cm long, 0.3–0.5 cm wide. Floral segments from strongly pointed (sharply acute) to rounded. Labellum 1.6 cm long, 1.0 cm wide, curved, variously striped or speckled with pale mauve to deep purple, or white; three-lobed, very narrow at the base, lateral lobes narrow, usually erect, and column embracing but occasionally flared outwards away from the column. Midlobe shape widely variable, occasionally two or three distinct shapes on the same plant, including oval, pointed spade, spade, broad heart and occasionally globular (similar to Table 6). Midlobe presentation 0.75–1.0 cm wide, forelobe presentation 0.4–0.65 cm wide. Callus on lamina green, yellow or colourless to white, with three low or distinctly elevated ridges, often conspicuously divided into three lobes at the anterior end. Apex of midlobe pointed or point absent, angled variously, often recurved. Column about 4 mm long, 3 mm wide, dilated laterally at the midportion and curved or angled sharply to an almost straight foot 0.5–0.9 cm long. Anther ovoid to subreniform viewed from above, pollinia slender, subequal, and falcate-obovoid. Nectary at base of column foot, from yellow to green in colour, most commonly green.

Distinctive aspects: There is a trend towards flowers with light to average substance and acute segments (starry), but there are some examples of large rounded flowers with heavy substance.

Notes: Characteristics intergrade with plants in the adjacent Coffs Harbour and Grafton areas at lower altitude, where pseudobulbs are shorter, and with plants at the western limit that are smaller and shorter, with

diminutive flowers. Intergrades with forms in the Border Ranges and with more southerly forms from the NSW north coast.

Chromosome number: Most plants diploid (2n=38); occasionally triploid (3n=57) (Adams 1992).

Grafton to Coffs Harbour forms

Description: Plants of variable habit, from compact to short or medium height, and widely open structure, either erect or spreading and scrambling. Aerial growths common. Pseudobulbs variable from very short (7 cm) to medium (14 cm) height, often narrow in the upper portion and at the apex, without specific identifying features, broadest (up to 1.4 cm) at the base and tapering upwards to a narrow apex (0.25–0.4 cm),segments 3–6, most commonly 5, when young, covered or partly covered with thin brown or green papery bracts which disintegrate with age to reveal green, brown or purple surface with longitudinal grooves. Leaves apical, up to 3–5 per pseudobulb, narrow, elliptical to ovate, 5–10 cm long, 1.3–2.1 cm wide. Colour usually mid green with or without red purple tints, the tints pronounced when plants are exposed to light; in erect plants there is a tendency towards very narrow leaves produced in a single plane, or variably twisted about the long axis. Plants variably floriferous, including multi-racemed pseudobulbs with dense floral displays. Flowers generally of moderate form and quality, with some attractive splash petal and pale mauve forms. Floral racemes 1 or 2, occasionally 3, arising terminally from the pseudobulbs and from lateral nodes between and below the origin of the leaves, racemes erect, semi-erect or semi-pendulous. Flowers 4–8 per raceme, median 6, on pedicels 5–10.5 cm long, peduncle variable from 5–10.5 cm long, rachis 3–8.5 cm long, inflorescence 8–20 cm long. Flower colour pure white to solid purple, most commonly splashed with purple and pale to mid-mauve with a mid to deep purple speckled labellum. Occasionally the labellum is almost solid purple. Flowers presenting cupped to planar, more commonly cupped and of light to medium substance, occasionally with a deeper colour on the reverse side. The mentum may be tinged with pale green or mauve-purple. Dorsal sepal 1.3–1.8 cm long, 0.5–0.6 cm wide, keel 1.5–2.6 cm long, lateral sepals spanning 2.3–3.2 cm, 0.9–1.3 cm wide, petals 1.0–1.5 cm long, 0.3–0.55 cm wide. Floral segments strongly pointed (sharply acute) to rounded. Labellum c. 1.6 cm long, 1.0 cm wide, curved, variously striped or speckled with pale mauve to deep purple, or white; three lobed, very narrow at the base, lateral lobes narrow, usually erect, and column embracing but occasionally flared outwards away from the column. Midlobe shape widely variable, occasionally two or three distinct shapes on the same plant, including oval, pointed spade, bilobed spade, spade, broad heart and occasionally globular (similar to Table 6). Midlobe presentation 0.65–0.95 cm wide, forelobe presentation 0.4–0.75 cm wide. Callus on lamina green, yellow or colourless to white, with three low or distinctly elevated ridges, often conspicuously divided into three lobes at the anterior end. Apex of midlobe pointed or point absent, angled variously, often recurved. Column generally 0.4 cm long, 0.3 cm wide, dilated laterally at the midportion and curved or angled sharply to an almost straight foot 0.5–0.9 cm long. Anther ovoid to subreniform viewed from above, pollinia slender, subequal, and falcate-obovoid. Nectary at base of column foot, from yellow to green, but most commonly green.

Distinctive aspects: There is a trend towards narrow upper portions of pseudobulbs and flowers with light to average substance and pointed segments, but there are some examples of large rounded flowers.

Notes: Characteristics intergrade with those of plants in the adjacent Dorrigo Gibraltar Range areas at higher altitude. Intergrades also occur with northern plants in the Border Ranges and with more southerly plants of the Hastings Region.

Chromosome number: Most plants diploid (2n=38); very occasionally triploid (3n=57) (Adams 1992).

Hastings to Comboyne forms

Description: Plants of miniature (very short) or short and compact habit or occasionally to medium height, often interweaving to form a mat with closed canopy over rocky outcrops, individual plants upright or spreading with widely radiating pseudobulbs. Aerial growths occasional. Pseudobulbs variable, from very short (4 cm) to medium (11 cm) height, usually robust, but sometimes more slender in the apical portion, broadest at the base (up to 1.4 cm diam.) and gradually tapering upwards to the apex (3–4 mm), segments 2–4, most commonly 3; when young, covered or partly covered with thin brown or green papery bracts which disintegrate with age to reveal a green, brown or purple surface with longitudinal grooves. Leaves apical, up to 3 or 4 per pseudobulb, narrow, elliptical to ovate, 3.5–10 cm long, 1.1–2.3 cm wide; colour usually grey green occasionally with a few red purple tints. Plants variably floriferous, usually with a medium density of flowers. Floral raceme(s) 1, sometimes 2, arising terminally from the pseudobulbs and rarely from lateral nodes between and below the origin of the leaves, racemes erect, semierect or pendulous. Flowers 2–8 per raceme, usually 4 or 5, on pedicels 1.0–1.5 cm long, peduncle variable from 3.5–8.3 cm long, rachis 3.5–9 cm long, inflorescence 8–14 cm long. Flowers pure white to deep mauve, occasionally *silcockii* colour (having white sepals and petals and purple markings on the labellum) and lavender. Flowers presenting cupped to planar, more commonly cupped and of medium to heavy substance. The mentum may be tinged with pale green or mauve. Dorsal sepal 1.1–1.9

cm long, 0.3–0.8 cm wide, keel 1.5–3.0 cm long, lateral sepals spanning 2.4–3.6 cm, 1.0–1.4 cm wide, petals 1.1–1.7 cm long, 0.3–0.7 cm wide. Floral segments from strongly pointed (sharply acute) to rounded, mostly tending to a relatively broad apex. Labellum approximately 1.5 cm long, 1.0 cm wide, curved, variously striped or speckled with pale mauve to deep purple, or white; three lobed, very narrow at the base, lateral lobes narrow, usually erect, and column embracing but occasionally flared outwards away from the column. Midlobe shape widely variable, often two or three distinct shapes on the same plant, including oval, pointed spade, spade, broad heart and occasionally globular or narrow heart (similar to Table 6). Midlobe presentation 0.6–1.1 cm wide, forelobe presentation 0.4–0.85 cm wide. Laminar callus green or yellow, with three low or distinctly elevated ridges, often conspicuously divided into three lobes at the anterior end. Apex of midlobe pointed or point absent, angled variously, often recurved. Column about 0.4, 0.3 cm, dilated laterally at the midportion and curved or angled sharply to an almost straight foot 0.5–0.9 cm long. Anther ovoid to subreniform viewed from above, pollinia slender, subequal, and falcate-obovoid. Nectary at base of column foot, from yellow to green, most commonly green.

Distinctive aspects: The grey green leaves are conspicuous in most but not all locations in this region, and the colour is relatively uniform in each population of plants.

Notes: The grey green leaf colour is distinctive at many locations in the region, but grades to mid green in adjacent regions, and is of variable intensity. Deep purple colour is uncommon. Flowers rarely have a significantly deeper colour on the reverse side. Characteristics intergrade with plants in the adjacent Coffs Harbour - Grafton areas to the north. Characteristics are usually distinguishable from inland plants of the Grafton - Manning region, but not in all cases.

Chromosome number: All plants tested have been diploid (2n=38) (Adams 1992).

Gloucester to Manning forms

Description: Plants short to medium height, infrequently tall and forming large congested clumps or growing as separate individuals, of widely variable habit, urn shaped to spreading, scrambling with horizontal and downward arching pseudobulbs. Aerial growths are common on some plants, but infrequent or absent on most. Pseudobulbs without specific identifying features, variable and usually robust, from short (6.5 cm) to long (35 cm), broadest (up to 2.8 cm) at the base and tapering upwards to a narrow apex (0.4 cm diam.), segments 2–5, most commonly 4; when young, covered or partly covered with thin brown or green papery bracts which disintegrate with age to reveal a green, brown or purple surface with longitudinal grooves. Leaves apical, 3–4 per pseudobulb, narrow, elliptical to ovate, 4.5–9 cm long, 1.4–2.1 cm wide. Colour usually mid green with or without red purple tints, the tints pronounced when plants are exposed to strong light. No absolute distinguishing leaf features, a tendency in many plants to robust leaves, variably twisted about the long axis. Plants variably floriferous, including a few multi-racemed pseudobulbs with dense floral displays. Flowers generally of moderate to excellent form and quality, with some outstanding forms in most of the main colours. Floral racemes 1–3, arising terminally from the pseudobulbs and occasionally from lateral nodes between and below the origin of the leaves, racemes erect to semierect. Three to ten flowers per raceme, median 6, on pedicels 1.0–1.5 cm long. Peduncle variable from 5–11.5 cm long, rachis 9–20 cm, total inflorescence 9–20 cm long. Flower colours pure white to solid purple, tending most commonly to pale to mid-mauve rarely with a slightly deeper colour on the reverse side, mid to deep purple speckled labellum. Occasionally the labellum is almost solid purple. Flowers presenting cupped to planar, more commonly cupped and of medium to very heavy substance. The mentum may be tinged with pale green or mauve purple. Dorsal sepal keel 1.9–3.0 cm long, dorsal sepal 1.1–2.2 cm long, 0.55–0.8 cm wide, lateral sepals spanning 2.2–4.1 cm, 1.1–1.4 cm wide, petals 1.1–1.8 cm long, 0.35–0.65 cm wide. Floral segments from pointed (acute) to rounded. Labellum approximately 1.6 cm long, 1.0 cm wide, curved, variously striped or speckled with pale mauve to deep purple; three lobed, very narrow at the base, lateral lobes narrow, usually erect, and column embracing but occasionally flared outwards away from the column. Midlobe shape widely variable, often two or three distinct shapes in a population and sometimes on the same plant, including oval, pointed oval, pointed spade, spade, bilobed spade, broad heart and globular (Table 6). Midlobe presentation 0.7–1.1 cm wide, forelobe presentation 0.45–0.75 cm wide. Callus on lamina green, yellow or colourless, with three low or distinctly elevated ridges, often conspicuously divided into three lobes at the anterior end. Apex of midlobe pointed or point absent, angled variously, often recurved. Column c. 0.4 cm long, 0.3 cm wide, dilated laterally at the midportion and curved or angled sharply to an almost straight foot 0.5–1.0 cm long. Anther ovoid to subreniform viewed from above, pollinia slender, subequal, and falcate-obovoid. Nectary at base of column foot, yellow to green, but most commonly green.

Distinctive aspects: There is a trend towards round shaped flowers with heavy substance and robust leaves which have a marked twist.

Notes: Characteristics intergrade with those of plants in adjacent areas to the north, and towards Bulahdelah in the south. Some plants of robust type are identifiable as coming from the region, but many are not.

Chromosome number: Most plants diploid (2n=38); occasionally triploid (3n=57) or tetraploid (4n=76). In some areas, purple flowering plants are exclusively triploid (Adams 1992).

Bulahdelah area forms

Description: Short compact plants crowded together forming large mats or growing as separate individuals. Aerial growths are occasional. Pseudobulbs variable, very short (4 cm) to short (8 cm), broadest at the base (up to 1.5 cm diam.) and tapering upwards to a variable apex (0.25–0.4 cm diam.), segments 2 or 3, most commonly 3; when young, covered or partly covered with thin brown or green papery bracts which disintegrate with age to reveal a green or brown surface with longitudinal grooves. Leaves apical, up to 4 per pseudobulb, most commonly 3, narrow, elliptical to ovate, 5.1–7.6 cm long, 1.3–2.0 cm wide. Colour usually mid green. Plants often with few flowers. Floral racemes, usually one, arising terminally from the pseudobulbs, rarely from lateral nodes between and below the origin of the leaves, racemes erect to semierect. Flowers 1–5 per raceme, median 3, on pedicels 1.0–1.4 cm long. Peduncle 4–8 cm long, rachis 3.5–7.0 cm long, inflorescence 8–14 cm long. Flowers pure white to mid mauve, most commonly pale mauve with a mid-purple speckled labellum and without deeper colour on the reverse side. Flowers presenting cupped, or occasionally planar and of medium substance. The mentum may be tinged with pale green or yellow. Dorsal sepal 1.2–1.7 cm long, 0.55–0.7 cm wide, keel 1.8–2.3 cm long, lateral sepals spanning 2.2–3.4 cm, 1.1–1.3 cm wide, petals 1.1–1.6 cm long, 0.3–0.5 cm wide. Floral segments pointed (sharply acute) to rounded. Labellum c. 1.6 cm long, 1.0 cm wide, curved, variously striped or speckled with pale mauve to deep purple, or white; 3-lobed, very narrow at the base, lateral lobes narrow, usually erect, or curved and column embracing. Midlobe shape widely variable, often 2 or 3 distinct shapes on the same plant, including oval, pointed spade, spade, narrow heart, broad heart and occasionally globular (similar to Table 6). Midlobe presentation 0.6–0.8 cm wide, forelobe presentation 0.4–0.6 cm wide. Callus on lamina green or yellow, with three low ridges, often conspicuously divided into three lobes at the anterior end. Apex of midlobe pointed or point absent, angled variously. Column c. 0.4 cm long, 0.3 cm wide, dilated laterally at the midportion and curved or angled sharply to an almost straight foot 0.5–0.9 cm long. Anther ovoid to subreniform viewed from above, pollinia slender, subequal, and falcate-obovoid. Nectary at base of column foot, yellow to green, but most commonly green.

Distinctive aspects: There is a trend towards very short plants with few small flowers of average substance and with rounded segments.

Notes: Characteristics intergrade with those of plants in the adjacent Hastings, Comboyne and Gloucester areas, where pseudobulbs are longer and flowering more prolific. Wide variations occur in this southern region, especially in the intergrading ranges between Bulahdelah and Gloucester, in flower colour, form, and plant growth habit.

Chromosome number: All plants tested have been diploid (2n=38) (Adams 1992).

Distribution and ecology: *Dendrobium kingianum* subsp. *kingianum* occurs in and around sclerophyll forest and rainforest from central coast NSW to the Sunshine Coast, north of Brisbane, Queensland. It is scattered and discontinuous due to its restricted habitat. At its northern limit it is found on the volcanic plugs of the Glasshouse Mountains and isolated communities north to Biggenden. Limiting factors in the north and west are likely the high temperatures or limited day length variation between summer and winter, restricting flowering, and the lower rainfall in the west. At the southern limit, lower winter temperatures may restrict growth. *Dendrobium kingianum* subsp. *carnarvonense* has a disjunct distribution well separated from subsp. *kingianum* and is found in sheltered gorges inland at the extreme north of the range, with relatively low evaporation rates, fairly constant humidity and adequate water.

Dendrobium kingianum grows as a lithophyte and rarely as an epiphyte in Eastern Australia from just north of the Hunter River (32°30'S) near Newcastle (Central NSW) to the Tropic of Capricorn (23°26'S) in central west Queensland. Small colonies at Isla Gorge, Biggenden, and the Monto area partially fill the gap in the range which was previously thought to exist between the Gympie and Biggenden area to the east and Carnarvon Gorge. The western limit follows the New England Highway in northern NSW and southern Queensland.

There are unconfirmed reports of *D. kingianum* (Clemesha 1965) outside of the substantiated range. These are possibly due to planting *D. kingianum* plants from private collections into the bush in areas south of the Hunter River and even in southern NSW and Victoria. Reports of plants of the "Bulahdelah form" south of the Hunter River at Ourimbah, Bucketty and Burragorang Valley prior to flooding by the Warragamba Dam, for example, may represent relocated plants.

Under favourable conditions *D. kingianum* forms extensive colonies on cliff faces and rocks in open forests or along forest creeks. There are places where it is the dominant plant species, covering north facing hillsides with plants up to several metres in diameter. Colonies may grow on rocky bluffs within a few kilometres of the sea, and at elevations of 3,000 feet in the Great Dividing Range. At the western limit small isolated colonies survive as moss embedded plants in dry country 100km west of the Great Divide and in an isolated population at Carnarvon Gorge (central Queensland) 450 km from the coast. Habitats include warm temperate rainforest, wet sclerophyll forests and dry forest types dominated by *Eucalyptus* species. Isolated restricted occurrences in the western and northern parts of the range suggest that the distribution was much more widespread in the past under wetter climates.

Dendrobium kingianum* subsp. *carnarvonense Peter B.Adams in P.B. Adams and S.D. Lawson, *Dendrobium kingianum*: *a unique Australian orchid*: 16 (1995)

Thelychiton carnarvonensis (P.B. Adams) M.A.Clem. & D.L.Jones, *The Orchadian* 13(11): 491 (2002)

Type: Carnarvon Gorge, Queensland, 14 Sep. 1994, *P.B. Adams 1135*; holo: BRI, iso: MEL.

Plants lithophytic and semiterrestrial, rarely epiphytic, with slender pseudobulbs, up to 15cm long, the older ones and lower portions of newer pseudobulbs covered by decomposing sandstone and leaf litter, the upper portions emergent and bearing frequent aerial growths, narrow at the apex. Leaves lanceolate, 8–14 cm long, 0.85–1.9 cm wide. Racemes erect or semierect, bearing 2–7 flowers groups towards the apex, segments curved to form a cup shaped flower, with purple blushing or striae on the reverse of sepals and on the labellum. Flowers small and round, 1.6 cm high 2.2 cm wide. Segments acute or subacute, forelobe and midlobe of labellum curved to form a narrow tube approximately 0.35–0.5 cm wide. Midlobe oval or broadly heart shaped, ending in a small point anteriorly, callus pale green without raised keels, ending bluntly or with three small nodules at the base of the midlobe.

Description: Plants forming dense mats of leafless pseudobulbs fully covered by sandy soil and debris, with the upper portions of more recent pseudobulbs emergent, bearing frequent aerial growths. Roots ramifying through soil and attached to rocks. Plants occasionally epiphytic. Pseudobulbs generally narrow at the base, 0.7–1.2 cm diam., and narrow to very narrow, 0.25–0.4 mm diam., at the apex; 9.0–15 cm long, curving irregularly in many different directions, segments 4–6, green in colour if aerial, yellow if subterranean, partly covered by a pale brown papery velum. Leaves apical, up to 3–4 per pseudobulb, narrow, lanceolate, 8.2–14 cm long, 0.85–1.9 cm wide, colour mid green with no purple tints. Plants variably floriferous, not usually forming dense displays. Floral racemes 1 or 2, arising from lateral nodes between and below the origin of the leaves, racemes erect or semierect. Flowers two to seven per raceme, median 4, clustered toward the floral apex on short pedicels 0.4–0.7 cm long. Peduncle 4.6–12 cm long, rachis 2.5–5 cm long, inflorescence 7–15 cm long. Flowers white anteriorly with purple striae or blush areas on reverse side of sepals. Labellum c. 1.2 cm long, 0.8 cm wide, curved, three lobed, narrow at the base, lateral lobes embracing the column. Labellum coloured mid purple or deep mauve speckles on a white background. Presenting cupped, round, of moderately heavy substance. Mentum white or tinged with pale green or mauve-purple. Dorsal sepal dorsal sepal 0.8–1.3 cm long, 0.4–0.6 cm wide, keel 1.65–2.2 cm long, lateral sepals spanning 1.6–2.2 cm, 0.85–1.0 cm wide, petals 0.7–1.2 cm long, 0.2–0.4 cm wide. Floral segments acute to subacute, sepals sometimes obtuse. Midlobe shape broad heart, oval, or pointed spade. Midlobe very narrow, 0.45–0.5 cm wide, forelobe also narrow, 0.35–0.4 cm wide. Callus on lamina pale green or yellow, a broad plate of tissue without clearly distinct keels, ending bluntly or with a suggestion of three nodules which may have a faint purple colouration. Apex of midlobe small, pointed. Column, anther, pollinia and stigma as for *D. kingianum* from other areas. Nectary at base of column foot, pale green or yellow.

Distinctive aspects: Partially subterranean habit, long narrow leaves, small and uniformly pale coloured flowers (occasionally with dark purple markings on the labellum), cup shaped with very narrow mid and fore lobe, and callus without keels or ridges.

Notes: Distinct from plants from other areas, most similar to the long-caned plants of southern Queensland and northern New South Wales, which have pale flowers with purple on the reverse side.

Chromosome number: unknown.

Distribution and ecology: Sandstone gorges of Central Queensland, between the Carnarvon region and Isla Gorge, usually in secluded, shaded situations near streams.

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References

Adams, PB (1988) Pollination of *Dendrobium kingianum* Bidw. and its natural hybrids – the role of fragrance and bee pollinators. *Symposium: Pollination 88*: 95–100. School of Botany, The University of Melbourne.

Adams, PB (1992) Chromosome analysis of some *Dendrobium kingianum* used in breeding programmes. *The Orchadian* 10, 300–303.

Adams, PB (2011) Systematics of Dendrobiinae (Orchidaceae), with special reference to Australian taxa. *Botanical Journal of the Linnean Society* 166, 105–126. https://doi.org/10.1111/j.1095-8339.2011.01141.x

Adams PB (2015) *Dendrobium bigibbum* (sect. *Phalaenanthe*) in Australia - analysis of diagnostic characters, review of taxa and a new classification. *Kew Bulletin* 70, 16. https://doi.org/10.1007/s12225-015-9565-x

Adams PB and Lawson SD (1995) *Dendrobium kingianum*. A unique Australian orchid. Central Queensland University Press, Rockhampton Queensland.

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Australian Ecology* 26, 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Anonymous (1883) Mr. Bailey's Paper, in Queensland Philosophical Society. *The Brisbane Courier* 38(8000), 7.

Bailey FM (1884) Contributions to the Queensland flora. *Proceedings of the Royal Society of Queensland* 1, 11–12.

Bailey FM (1902) *The Queensland Flora* 5: 1528. Government Printer, Brisbane.

Bailey FM (1905) Contributions to the flora of Queensland. *Queensland Agricultural Journal* 15, 781.

Bentham G (1873) *Flora Australiensis. Volume 6.* L. Reeve & Co: London.

Burke JM, Bayly MJ, Adams PB, and Ladiges PY (2008) Molecular phylogenetic analysis of *Dendrobium* (Orchidaceae), with emphasis on the Australian section *Dendrocoryne*, and implications for generic classification. *Australian Systematic Botany* 21, 1–14. https://doi.org/10.1071/SB07038

Burke JM, Ladiges PY, Batty EL, Adams PB, Bayly MJ (2013) Divergent lineages in two species of *Dendrobium* orchids (*D. speciosum* and *D. tetragonum*) correspond to major geographical breaks in eastern Australia. *Journal of Biogeography* 40, 2071–2081. https://doi.org/10.1111/jbi.12145

Clements MA (1989) Catalogue of Australian Orchids. *Australian Orchid Research* 1, 1–160.

Clements MA (2003) Molecular Phylogenetic Systematics in the Dendrobiinae (Orchidaceae), with emphasis on *Dendrobium* sect. *Pedilonum*. *Telopea* 10, 247–298. https://doi.org/10.7751/telopea20035619

Clements MA and Jones DL (2002) Nomenclatural changes in the Dendrobieae (Orchidaceae) 1: The Australasian region. *The Orchadian* 13, 485–497.

Clemesha S (1965) *Dendrobium kingianum* Bidw. from north to south. *The Orchadian* 2, 34–36.

Darriba D, Taboada GL, Doallo R, Posada D (2012) JModelTest 2: More models, new heuristics and prallel computing. Nature methods 9, 772.

Das S, Baumgartner JB, Esperon-Rodriquez M, Wilson PD, Yap JYS, Rossetto M, Beaumont LJ (2019) Identifying climate refugia for 30 Australian rainforest plant species, from the last glacial maximum to 2070. *Landscape Ecology* 34, 2883–2896. https://doi.org/10.1007/s10980-019-00924-6

Dixon P (2003) VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science* 14, 927–930. https://doi.org/10.1111/j.1654-1103.2003.tb02228.x

Dockrill AW (1992) *Australian indigenous orchids.* The Society for Growing Australian Plants, Sydney.

Dryden IL, Mardia KV (1998) *Statistical Shape Analysis*. (Wiley: Chichester, UK)

Fahey M, Rosetto M, Wilson PD, Ho SYW (2019) Habitat preference differentiates the Holocene range dynamics but not barrier effects on two sympatric, congeneric trees (*Tristaniopsis*, Myrtaceae). *Heredity* 123, 532–548. https://doi.org/10.1038/s41437-019-0243-x

Heslewood MM, Lowe AJ, Crayn DM, Rossetto M (2014) Contrasting levels of connectivity and localised persistence characterise the latitudinal distribution of a wind-dispersed rainforest canopy tree. *Genetica* 142, 251–264. https://doi.org/10.1007/s10709-014-9771-8

Kotilínek M, Tesitelová T, Kosnar J, Fibich P, Hemrová L, Koutecky, Münzbergova Z, Jersaková J (2020) Seed dispersal and realized gene flow in two forest orchids in a fragmented landscape. *Plant Biology* 22, 522–532. https://doi.org/10.1111/plb.13099

Kruskal JB (1964) Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 290, 115–129. https://doi.org/10.1007/BF02289694

Li D, Li Z-J, Mao P, Yan X-F, Chun Z, Ma X-R (2012) Phylogenetic analysis and identification of *Dendrobium* species based on ribosomal DNA internal transcribed spacer (ITS) Sequence. *Yuan Yi Xue Bao*39, 1539–1550.

Li J, Gale SW, Kumar P, Zhang J, Fischer G (2018) Prioritizing the orchids of a biodiversity hotspot for conservation based on phylogenetic history and extinction risk. *Botanical Journal of the Linnaean Society* 186, 473–497. https://doi.org/10.1093/botlinnean/box084

Lindley J (1844) Miscellaneous matter of the Botanical Register. *Edwards Botanical Register* 30, 1–92.

Lindley J (1845) *Dendrobium kingianum*. *Edwards Botanical Register* 31, 61. https://www.biodiversitylibrary.org/item/9068#page/174/mode/1up

Martin HA (2006) Cenozoic climatic change and the development of the arid vegetation in Australia. *Journal of arid Environments* 66, 533–563. https://doi.org/10.1016/j.jaridenv.2006.01.009

Milligan GW and Cooper MC 1988 A study of standardisation of variables in cluster analysis. *Journal of Classification* 5, 181–204. https://doi.org/10.1007/BF01897163

van den Berg C, Goldman DH, Freudenstein JV, Pridgeon AM, Cameron KM, Chase MW (2005) An overview of the phylogenetic relationships within Epidendroideae inferred from multiple DNA regions and recircumscription of Epidendreae and Arethuseae (Orchidaceae). *American Journal of Botany* 92, 613–624. https://doi.org/10.3732/ajb.92.4.613

von Mueller F (1862) *Fragmenta phytographiæ Australiæ. v.3 1862–63*.Auctoritate Gubern. Coloniæ Victoriæ, Ex Officina Joannis Ferres, Melbourne.

Olson CL (1974) Comparative robustness of six tests in multivariate analysis of variance. *Journal of the American Statistical Association* 69, 894–908. https://doi.org/10.1080/01621459.1974.10480224

Pridgeon AM, Cribb PJ, Chase MW, Rasmussen FN (eds) 2014 *Genera Orchidacearum Volume 6: Epidendroideae (Part 3)*. Oxford University Press, United Kingdom.

R Core Team (2018) R: A language and environment for statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rambaut A (1996) 'Se-Al: sequence alignment editor' http://evolve.zoo.ox.ac.uk

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19, 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biologty* 61, 539–542. https://doi.org/10.1093/sysbio/sys029

Rossetto M, Kooyman R, Sherwin W, Jones R (2008) Dispersal limitations, rather than bottlenecks or habitat specificity, can restrict the distribution of rare and endemic rainforest trees. *American Journal of Botany* 95, 321–329.

Rupp HMR (1943) *The Orchids of New South Wales*. National Herbarium, Sydney.

Rutherford S, Rossetto M, Bragg JG, McPherson H, Benson D, Bonser SP, Wilson PG (2018) Speciation in the presence of gene flow: population genomics of closely related and diverging *Eucalyptus* species. *Heredity* 121, 126–141. https://doi.org/10.1038/s41437-018-0073-2

Sand-Jensen K, Hammer KJ (2012) Moss cushions facilitate water and nutrient supply for plant species on bare limestone pavements. *Oecologia* 170, 305–312. https://doi.org/10.1007/s00442-012-2314-z

Simpson L, Clements MA, Crayn DM, Nargar K (2018). Evolution in Australia's mesic biome under past and future climates: Insights from a phylogenetic study of the Australian rock orchids (*Dendrobium speciosum* complex, Orchidaceae). *Molecular Phylogenetics and Evolution* 118, 32–46. https://doi.org/10.1016/j.ympev.2017.09.004

Singh HK, Parveen I, Raghuvanshi S, Babbar SB (2012) The loci recommended as universal barcodes for plants on the basis of floristic studies may not work with congeneric species as exemplified by DNA barcoding of *Dendrobium* species. *BMC Research Notes* 5, 42. https://doi.org/10.1186/1756-0500-5-42

Sklenár P, Kucerová A, Macková J, Romoleroux K (2016) Temperature microclimates of plants in a tropical alpine environment: how much does growth form matter? *Arctic, Antarctic and Alpine Research* 48, 61–78. https://doi.org/10.1657/AAAR0014-084

Sneath PHA, Sokal RH (1973) *Numerical taxonomy: the principles and practice of numerical classification*. WH Freeman and Co, San Francisco.

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30, 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Takamiya T, Wongsawad P, Tajima N, Shioda N, Lu JF, Wen CL, Wu JB, Handa T, Iijima H, Kitanaka S, Yukawa T (2011) Identification of *Dendrobium* species used for herbal medicines based on ribosomal DNA internal transcribed spacer sequence. *Biological Pharmaceutical Bulletin* 34, 779–782. https://doi.org/10.1248/bpb.34.779

Takamiya T, Kitamura S, Suzuki S, Shioda N, Matsuo Y, Murase K, Kaiho Y, Tsurumaki Y, Fujiwara Y, Sone M, Machida T, Matsumoto R, Miyamoto A, Hirose D, Furukawa M, Makino M, Matsuzaki K, Kitanaka S, Yukawa T, Iijima H (2018) Identification of two Phenanthrene derivatives from Australasian allied species in genus *Dendrobium*. *Chemical Pharmaceutical Bulletin* 66, 642–650. https://doi.org/10.1248/cpb.c18-00076

Tsai CC, Peng CI, Huang SC, Huang PL, Chou CH (2004) Determination of the genetic relationship of *Dendrobium* species (Orchidaceae) in Taiwan based on the sequence of the internal transcribed spacer of ribosomal DNA. *Scientia Horticulturae*101, 315–325. https://doi.org/10.1016/j.scienta.2003.11.004

Upton WT (1989) *Dendrobium Orchids of Australia*. Timber Press, Portland, Oregon.

Van Der Wal J, Shoo LP, Williams SE (2009) New approaches to understanding late Quaternary climate fluctuations and refugial dynamics in Australian wet tropical rain forests. *Journal of Biogeography* 36, 291–301. https://doi.org/10.1111/j.1365-2699.2008.01993.x

Veitch JH (1887) A Manual of Orchidaceous Plants 1(3), 52.

Warner R, Williams BS (1888) The Orchid Album, Volume 7. BS Williams: Victoria and Paradise Nurseries, Upper Holoway.

Whitehead MR, Sherwin WB, Crayn DM, Rossetto M (2019) A predominantly southern distribution conceals a northern reservoir of diversity in a wet sclerophyll tree. *Australian Journal of Botany* 67, 455–462. https://doi.org/10.1071/BT19065

World Checklist of Selected Plant Families. https://wcsp.science.kew.org/ Accessed 27th August 2020.

Zotz G, Schweikert A, Jetz W, Westerman H (2000) Water relations and carbon gain in relation to cushion size in the moss *Grimmia pulvinata* (Hedw.) Sm. *New Phytologist* 148, 59–67. https://doi.org/10.1046/j.1469-8137.2000.00745.x

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A new and substrate specific species of *Ilex* (Aquifoliaceae) from north-eastern Queensland, Australia

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Abstract

Ilex corymbosa A.J.Ford & Halford is formally described and illustrated, with notes on habitat, distribution, conservation status and how to distinguish it from *I. arnhemensis*, the only other native species of *Ilex* in Australia.

Introduction

Ilex L. is the sole genus within Aquifoliaceae and it is estimated to include more than 664 species of dioecious trees and shrubs (Yao *et al.* 2020). The genus is widely distributed throughout the tropics and temperate zones, with centres of species diversity in east Asia and the tropical Americas (Stevens 2001; Xu *et al.* 2017; Yao *et al.* 2020).

In Australia, *Ilex* is represented by two species (Pedley 1984). The one named species, *Ilex arnhemensis* (F.Muell.) Loes., has two geographically separated subspecies which both predominantly inhabit riparian rainforest vegetation in northern Australia. The other species listed by Pedley (1984) is an undescribed species of *Ilex* from north-east Queensland. This species has been represented in Australian herbaria for more than 50 years and was first alluded to in the card key to the rainforest trees of north Queensland (Hyland 1971). Until recently only mature male flowers and a few immature fruit were known, even though it occurs in multiple locations. Female flowers and mature fruits have recently been collected, enabling a full description to be made and we describe this species below as *I. corymbosa* A.J.Ford & Halford.

Material and Methods

This study of *Ilex* was based on the examination of herbarium specimens held at BRI and CNS. These specimens also include the valuable spirit (alcohol) preserved collection at CNS. In addition, fieldwork by the first author enabled the collection of fresh material (both male and female) for morphological assessment as well as pertinent ecological information.

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Taxonomy

Ilex corymbosa A.J.Ford & Halford, *sp. nov.*

Type: Queensland: Cook District: Tam O'Shanter Forest Reserve, off Lacey Creek walking track towards Licuala, NW of Mission Beach, 28 Aug 2019, *A. Ford 6746* & *W. Cooper* (holotype: BRI; isotypes: CNS 149564.1, CNS 149564.2, *distrubiendi*).

Ilex sp. Gadgarra (B.P.Hyland RFK2011) [Hyland *et al.*, 2010].

Ilex sp. (Gadgarra B.P.Hyland RFK2011) [Jessup 1994, p.23; Jessup & Halford 2020.

Ilex sp. (Gadgarra) [Cooper 2004, p. 58].

Ilex sp. [Pedley 1984, p. 202].

Ilex sp. [Hyland 1971].

Illustrations: Cooper (2004: 58), as *Ilex* sp. (Gadgarra).

Evergreen dioecious trees to 30 m high with diameter at breast height up to 60 cm; trunk terete to fluted usually buttressed at base; bark flaky to fissured or lacking any distinguishing features. Young leafy branchlets purplish, terete to angled, longitudinally striated, clothed in moderately dense, very short whitish antrorse hairs (*c.* 0.1 mm long). Adult branchlets and branches creamy-grey, usually with conspicuous globose and whitish lenticels. Stipules (moderately persistent) triangular, 0.1–1 mm long, inconspicuous. *Leaves* alternate, petiolate; petiole 4–8 mm long, channelled adaxially, longitudinally striated abaxially, purplish when young and ageing to green; lamina chartaceous, elliptic to elliptic-obovate, 5.8–11.5 cm long, 2.1–4.3 cm wide, length to width ratio 2.1–3:1, glabrous; base attenuate; margin entire (see notes for juvenile leaf description); apex acute to acute-acuminate, with or without a distinctive mucro *c.* 0.4 mm long; midvein in fresh and dried material impressed adaxially (rarely flush), prominently raised abaxially (more so proximally); secondary veins 8–12 on each side of the midvein, brochidodromous, flush to slightly impressed adaxially and raised abaxially in fresh material, raised on both surfaces when dried; tertiary venation scarcely discernible when fresh or dried. Inflorescences fasciculate consisting of cymes or solitary flowering units in leaf axils of one-year old growth, rarely ramiflorus or on new growth. *Male inflorescence* with 7–14 cymes; cymes 1–3-flowered, peduncles 1.1–9 mm long; rachis 1–4 mm long; bracts basal, *c.* 1.1 mm long, deltoid, puberulent; subtending flower bract 0.4–0.5 mm long, triangular, glabrous to sparsely puberulent; sub-basal bracteoles when present *c.* 0.5 mm long; pedicels 1.9–3.6 mm long, *c.* 0.4 mm diameter, puberulent, sparsely clothed in very short arching antrorse hairs. *Flowers* actinomorphic, 7–8 mm diameter at anthesis. *Calyx* 4–6-lobed (occasionally with vestigial or poorly formed lobes when 4-lobed), green; calyx tube much shorter than the lobes; lobes ovate, 0.7–1.1 mm long, 0.6–1.1 mm wide, glabrous on both surfaces, margin ciliate. *Corolla* whitish, shortly connate basally; tube *c.* 0.5 mm long; lobes 4–6, imbricate, spreading at anthesis, broadly oblong-elliptic, boat-shaped, 1.9–2.9 mm long, 1.5–2.5 mm wide, glabrous on both surfaces, margin shortly ciliate. *Stamens* 4–6, inserted at corolla lobe sinuses; filaments 0.8–1.9 mm long, glabrous; anthers ovate 1–1.4 mm long, *c.* 0.8 mm wide, dehiscing laterally through longitudinal slits. *Rudimentary ovary* ovoid, glandular-papillose, apex beaked. *Female inflorescence* 1–8-flowered, peduncles *c.* 1.1 mm long; rachis 1–2 mm long; pedicels *c.* 5.2 mm long, *c.* 1 mm diameter, puberulent with short, antrorse hairs; bracts *c.* 1 mm long, sub-basal bracteoles *c.* 1 mm long. *Flowers* actinomorphic, 8–9 mm diameter. *Calyx* 4–6-lobed, calyx tube much shorter than the lobes; lobes broadly ovate, 0.8–0.9 mm long, 1.1–1.4 mm wide, sparsely puberulent abaxially, margin ciliate, green. *Corolla* whitish, shortly connate basally; tube *c.* 0.3 mm long; lobes 4–6, imbricate, spreading at anthesis, broadly oblong-elliptic, boat-shaped, 3–3.5 mm long, 2.7–2.9 mm wide, glabrous on both surfaces, margin shortly ciliate. *Staminodes* 4–6, inserted at corolla lobe sinuses; filaments *c.* 1.5 mm long, glabrous; sterile anthers *c.* 0.5 mm long. *Ovary* shortly ellipsoid, glabrous, 4–6-locular, each locule with one distally inserted ovule, *c.* 1.7 mm high, *c.* 1.8 mm diameter; stigma sessile, mammilliform-turbinate, sticky. *Fruit* a drupe, fleshy, globose to depressed globular (sometimes laterally compressed), 6–7 mm long, 7–8.5 mm diameter, glabrous, red when ripe (changing from yellow-orange), calyx persistent, apex crowned by 4–6 persistent stigmas; pyrenes 4–6, 1–locular, creamy yellow, 5–6 mm long, endocarp thick and bony, abaxial surface longitudinally 3–5-grooved. *Seed* curved, 3-faced, 4–5 mm long, outer testa completely covered with densely packed wavy striations, inner testa thin and brown, endosperm starchy. *Embryo c.* 0.4 mm long, radicle about the same length as the cotyledons. Specific wood density 587 kg/m^3. *White Sassafras.* (Figure 1)

Fig. 1. *Ilex corymbosa*. A. Male inflorescence habit and showing purple petioles on new growth. B. Male inflorescence habit on one year old twigs. C. Ramiflorus male inflorescence and showing white lenticels on three year old branchlets. D. Female inflorescence habit. E. Mature fruit. F. Trunk from a canopy tree 30 cm dbh. (Photo credits; A: Rigel Jensen; E: Wendy Cooper; B, C, D and F: Andrew Ford).

Diagnosis: *Ilex corymbosa* differs from *Ilex arnhemensis* by having: puberulent leafy twigs (*vs* glabrous), shorter corolla lobes in male flowers (1.9–2.9 *vs* 3.2–4 mm long), shorter filaments in male flowers (0.8–1.9 *vs c.* 2.5 mm long), staminodes present in female flowers (*vs* absent), corolla well-formed in female flowers (*vs* vestigial), inflorescences fasciculate (*vs* non-fasciculate), fruit red (*vs* green-cream) and fewer number of pyrenes per fruit (4–6 *vs* 12–16).

Distribution: Endemic to the Wet Tropics bioregion (Department of Environment 2012) in north-eastern Queensland, Australia, where it is currently known from a restricted area between the eastern edge of the Atherton Tableland (near Malanda) and Mission Beach (east of Tully) (Figure 2).

Habitat and Ecology: This species is recorded from the lowlands and coastal foothills to sub-mountainous areas in very high rainfall (> 3,000 mm per annum) locations within mesophyll to notophyll rainforests on heavy clay soils derived exclusively from metamorphic substrates. Types of metamorphic rocks include: schist, quartzite and mudstones. Common canopy species throughout most of its range include: *Balanops australiana, Beilschmiedia bancroftii, Beilschmiedia oligandra, Cardwellia sublimis, Carnarvonia araliifolia, Ceratopetalum virchowii, Cryptocarya oblata, Endiandra montana, Flindersia* spp., *Garcinia zichii, Musgravea heterophylla, Musgravea stenostachya, Monoon patinatum, Syzygium endophloium* and *Syzygium kuranda*. Common small trees and shrubs include: *Acronychia vestita, Antirhea tenuiflora, Apodytes brachystylis, Atractocarpus* spp., *Chionanthus axillaris, Citronella smythii, Gossia myrsinocarpa, Pilidiostigma tropicum, Steganthera laxiflora, Psychotria* spp. and *Toechima erythrocarpum*. Altitudinal range from near sea-level to 840 m.

Phenology: This species has been very sparingly collected when fertile, with most specimens being sterile. Flowering material is recorded for August–September and mature fruit is known from November.

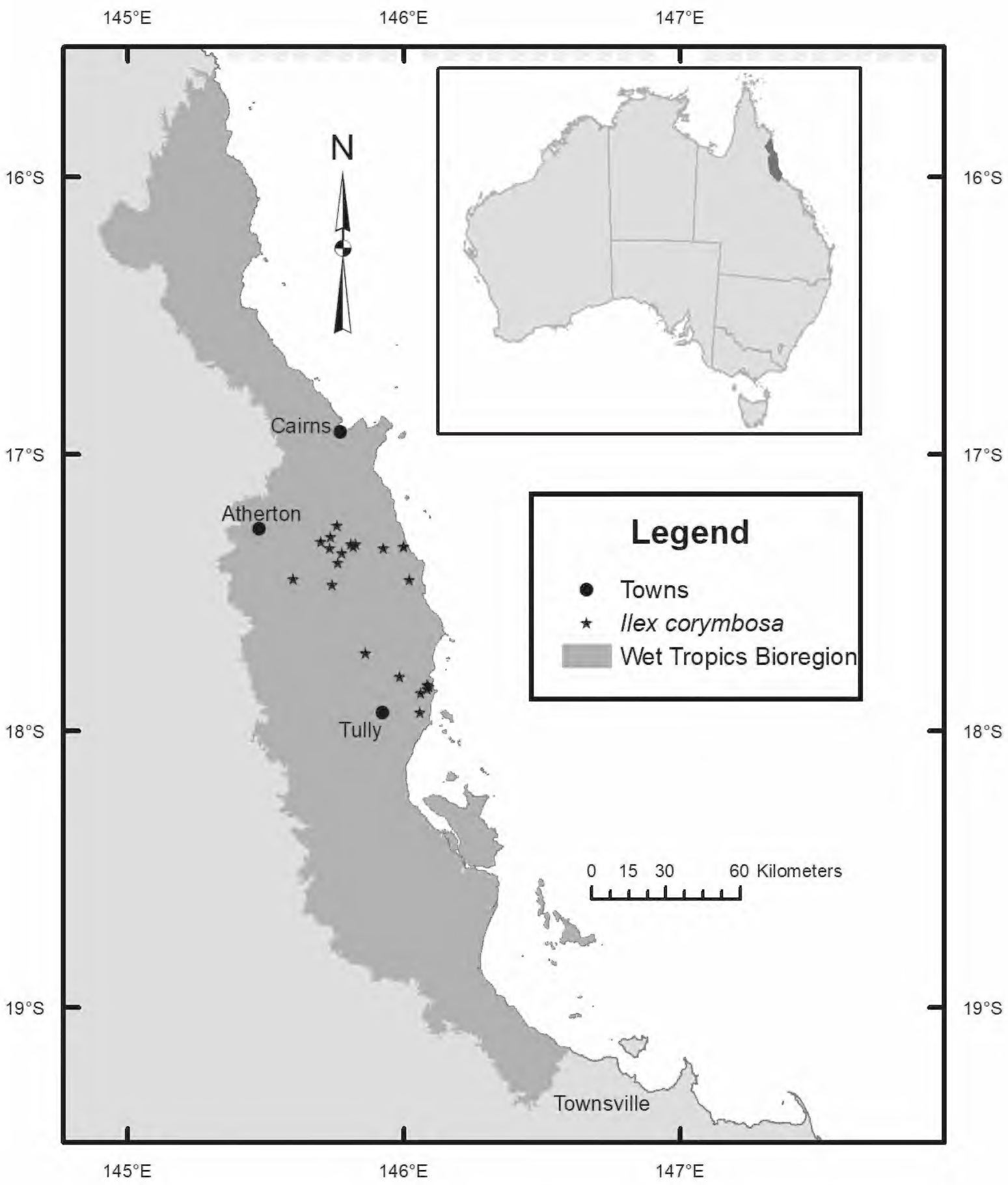

Fig. 2. Distribution of *Ilex corymbosa* in north-east Queensland, Australia.

Conservation status: *Ilex corymbosa* is yet to be evaluated against the International Union for the Conservation of Nature criteria (IUCN 2019). The species has an estimated extent of occurrence of only 1620 km^2. There is limited evidence to support a decline in population even though the quality of the habitat has been dramatically compromised by severe cyclonic activity in the past 15 years. Further fieldwork is required to assess recruitment activity, population numbers and any threats to the species.

Etymology: The specific epithet is derived from the Latin *corymbosus* and alludes to the clustered flowers and fruits of this species.

Affinities: At a gross morphological level *Ilex corymbosa* would appear to be most closely related to the other Australian species, *I. arnhemensis.* A comparison of diagnostic differences between the two native species in Australia is provided in Table 1. However, sexual dimorphism is extreme with *I. arnhemensis* having a vestigial and caducous corolla in pistillate flowers which seemingly perform no function as they do not enclose the ovary even when the buds are primordial. Pistillate flowers of *I. corymbosa* on the other hand are well-formed with an enclosing corolla and staminodes which exhibit cryptic dioecy (Eckhart 1999).

Sexual dimorphism is strongly exhibited in the two Australian species of *Ilex*, with the inflorescence types being strictly sexually differentiated between and within both species. *Ilex arnhemensis* has a solitary (sensu Hu 1949) inflorescence structure with males usually having a dichotomous compound cyme or a 3-flowered simple cyme to a long-pedicellate solitary flower. Female inflorescences are either a 3-flowered simple cyme or a short-pedicellate solitary flower. *Ilex corymbosa* has a fasciculate (sensu Hu 1949) inflorescence structure with males having many 1–3-flowered individual branches, whereas females occur in 1-flowered individual branches only.

To date there are two published *Ilex* phylogenetic studies, both using plastid and nuclear markers to infer relationships (Manen *et al.* 2010 and Yao *et al.* 2020). The data presented by Manen *et al.* (2010) (figures 3 and 4 pages 963 to 964) included the two Australian species and placed them in the "Indico-malaicae alliance", which includes species from South-East Asia and New Caledonia. The two Australian species were not found to be sister species and *I. arnhemensis* was inferred to be more closely related to *I. wallichii* Hook.f., a species that occurs in Indo-China to Peninsula Malaysia (Manen *et al.* 2010). The evolutionary relationships of *I. corymbosa* with the other species in the Indico-malaicae alliance was not resolved with the work of Manen *et al.* (2010) and it was not included in the dated phylogeny of Yao *et al.* (2020). The fossil calibrated molecular dates indicated that *I. arnhemensis* derived post-Miocene from within a largely South-East Asian clade of species with entire leaf margins (Yao *et al.* 2020). While the fossil pollen records suggest that *Ilex* was once widespread in Australia during the upper Cretaceous to late Miocene (Martin 1977) the current molecular data do not suggest that either of the Australian species are ancient relicts but more likely originated from more recent independent introductions from Sunda. While the molecular phylogenies are not fully resolved both the nuclear and plastid markers suggest multiple movements of *Ilex* into South-East Asia, all likely from within Eastern Asia. Further work is needed to understand the species level relationships of *I. corymbosa* within the South-East Asian clade and this will require sampling across this region, enabling further understanding of the floristic exchange between Sunda and Sahul.

Table 1. Morphological comparison between *Ilex corymbosa and I. arnhemensis*.

	I. corymbosa	*I. arnhemensis*
Leafy twig indumentum	puberulent	glabrous
Male flower corolla lobe length (mm)	1.9–2.9	3.2–4
Filament length (mm)	0.8–1.9	*c.* 2.5
Female flower corolla	well-formed	vestigial
Female flower staminodes	present	absent
Inflorescence	fasciculate	non-fasciculate
Fruit colour at maturity	red	green to cream
Pyrenes/fruit	4–6	12–16
Pyrene ornamentation	3–5-grooved	1-grooved
Pyrene length (mm)	5–6	*c.* 2.3

Notes: Freshly expanding new growth and current leaves have petioles and leafy twigs which are purplish. This feature is lost upon drying. Older leaves and leafy twigs also lose this purple colouration. Newly expanding leaves are pale green.

Seedling and sapling leaves of *Ilex corymbosa* have infrequent teeth [*Ford et al. 2966* (CNS) and *Ford et al. 3616* (CNS)]. In the field the combination of toothed leaves and purplish petioles makes this species a candidate for one of the many co-occurring species of *Symplocos*. However, *Ilex* has stipules and chartaceous leaves whereas *Symplocos* lack stipules and their leaves are coriaceous. The seedling leaves of *Ilex arnhemensis* subsp. *arnhemensis* (*Hyland 25157RFK*; CNS) and *I. arnhemensis* subsp. *ferdinandi* (*Hyland 13437*; CNS) both have toothed leaf margins.

Ripe fruit are red, but before maturity they change from yellow to yellow-orange before finally turning red.

Ilex corymbosa has been only recorded on metamorphic substrates, although there are extensive areas of granite, basalt and alluvium within the species range. For example, it occurs on the Seymour Range near Innisfail and then next occurs to the west on the eastern edge of the Atherton Tableland, thus, avoiding the alluvial coastal plain, the lowland to upland granites and the lowland basalts. The metamorphic rocks are from a variety of ages and origins, including units from the Hodgkinson and Barnard Provinces (Bain and Draper, 1997).

Although not mentioned, the voucher specimen that was used for *Ilex* sp. nov. (Manen *et al.* 2010, pp. 962 and 964) is referable to *Ford et al. 2967* (CNS). This sample was sent to Lyn Craven who forwarded it to J.-F. Manen directly, without the collection details being acknowledged.

Additional specimens seen: QUEENSLAND: Cook District: SFR 310, Gadgarra, 3 Oct 1968, *B. Hyland 2011RFK* (BRI, CNS); NPR 904, Wooroonooran, along 'Donkey Track' off Russell River Track, site 29, above Chuck Lunga Creek, 4 Oct 2001, *A. Ford 2967 et al.* (BRI, CNS); Trail into *Stockwellia* site near Malanda, 4 Feb 2009, *C. Costion 1699* (BRI, CNS); NPR 904 Wooroonooran, *c.* 700m S of Towalla Mine, above Coolamon Creek, site 33, 30 Oct 2001, *A. Ford 3035 et al.* (BRI, CNS); Japoon National Park, Liverpool Creek area off Warrakin Road, Japoon, 19 Dec 2007, *A. Ford 5183* (BRI, CNS); Australian Insect Farm, Seymour Range, NNW of Daradgee, site 70, 10 Sep 2002, *A. Ford 3616 et al.* (BRI, CNS); Japoonvale NP, off end of Shell Pocket

Road, El Arish, 18 Oct 2006, *A. Ford 4871* and *H. Murphy* (BRI, CNS); Dirran River, 3 Mar 2002, *R. Mazlin 2* (CNS); SFR 1137, Mission Beach, 15 Nov 1963, *B. Hyland 767RFK* (BRI, CNS); Mission Beach, 16 Oct 1967, *B. Hyland 1150RFK* (BRI, CNS); *loc. cit.*, 16 Oct 1967, *B. Hyland 1153RFK* (BRI, CNS); *loc. cit.*, May 1968, *H.E. Volck AFO s.n.* (QRS 502867) (CNS); Wyvuri, Cape York region, 11 Jul 1974, *B. Hyland 3060RFK* (BRI, CNS); Wyvuri Holding, E of Babinda, 26 Jun 1968, *B. Hyland 1541RFK* (BRI, CNS); Tam O'Shanter Forest Reserve, off Lacey Creek walking track towards Licuala, NW of Mission Beach, 16 Nov 2019, *W. Cooper 2610* and *T. Tuck* (CNS); *loc. cit.*, 28 Aug 2019, *A. Ford 6745* and *W. Cooper* (BRI, CNS): North Kennedy District: Tam O'Shanter NP, low slope of Mt Douglas, off Tully-Mission Beach Road, site 151, 8 Mar 2007, *A. Ford 4965* (BRI, CNS); Tam O'Shanter FR, along the southern Lacey Creek walking track, *c.* 1km from Jurs Creek crossing, west of Mission Beach, 6 May 2005, *A. Ford 4646* (BRI, CNS).

Key to the native species of *Ilex* in Australia

1. Leafy twigs puberulent; inflorescences fasciculate; female flowers with conspicuous corolla, staminodes present; male flowers with corolla lobes 1.9–2.9 mm long, filaments 0.8–1.9 mm long; fruit red with 4–6 pyrenes ..... **I. corymbosa**

1: Leafy twigs glabrous; inflorescences non-fasciculate; female flowers with vestigial corolla, staminodes absent; male flowers with corolla lobes 3.2–4 mm long, filaments *c.* 2.5 mm long; fruit green to cream with 12–16 pyrenes ..... **I. arnhemensis**

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References

Bain JHC, Draper JJ (1997) North Queensland geology, *Australian Geological Survey Organisation Bulletin 240, and Queensland Department of Mines and Energy Queensland Geology 9.* (Queensland Department of Mines and Energy, Brisbane)

Cooper W (2004) *Fruits of the Australian tropical rainforest*. (Nokomis Editions, Melbourne)

Department of the Environment (2012) *Interim Biogeographic Regionalisation for Australia, Version 7.* http://www.environment.gov.au/land/nrs/science/ibra [accessed 23 August 2019].

Eckhart VM (1999) Sexual dimorphism in flowers and inflorescences. In: Geber MA, Dawson TE, Delph LF (eds) *Gender and sexual dimorphism in flowering plants*. pp. 123–148. (Springer, Berlin, Heidelberg) https://doi.org/10.1007/978-3-662-03908-3_5

Hu S (1949) The genus *Ilex* in China. *Journal of the Arnold Arboretum* 30: 233–344. https://doi.org/10.5962/bhl.part.18050

Hyland BPM (1971) *A card key to the rain forest trees of north Queensland.* (Department of Forestry, Brisbane)

Hyland BPM, *et al.* (2010) *Australian tropical rainforest plants, 6th edition*. http:///www.anbg.gov.au/cpbr/cd-keys/rfk/index.html [accessed 23 August 2019]

IUCN Standards and Petitions Subcommittee (2019) *Guidelines for using the IUCN Red List categories and criteria*. Version 14. Prepared by the Standards and Petitions Subcommittee. http://www.iucnredlist.org/documents/RedListGuidelines.pdf

Jessup LW (1994) Aquifoliaceae. In Henderson RJF (ed.) *Queensland Vascular Plants: Names and Distribution.* (Queensland Herbarium, Brisbane)

Jessup LW, Halford JJ (2020). Aquifoliaceae. In Brown GK & Bostock PD (eds), *Census of the Queensland Flora 2020*. (Queensland Department of Environment and Science, Brisbane) https://www.data.qld.gov.au/dataset/census-of-the-queensland-flora-2020 [accessed 24 February 2021]

Loizeau PA, Savolainen V, Andrews S, Barriera G, Spichiger R (2016) Aquifoliaceae. In: Kadereit J., Bittrich V. (eds) *Flowering plants. Eudicots. The families and genera of vascular plants*, vol 14. pp. 31–36. (Springer, Cham) https://doi.org/10.1007/978-3-319-28534-4_3

Manen J-F, Barriera G, Loizeau P-A, Naciri Y (2010) The history of extant *Ilex* species (Aquifoliaceae): evidence of hybridization within a Miocene radiation. *Molecular Phylogenetics and Evolution* 57: 961–977. https://doi.org/10.1016/j.ympev.2010.09.006

Martin HA (1977) The history of *Ilex* (Aquifoliaceae) with special reference to Australia: evidence from pollen. *Australian Journal of Botany* 25: 655–673. https://doi.org/10.1071/BT9770655

Pedley L (1984) Aquifoliaceae. In George, AS (ed.) *Flora of Australia, Volume 22, Rhizophorales to Celastrales.* pp. 199–204. (Australian Government Printing Service, Canberra)

Stevens PF (2001 onwards). Angiosperm phylogeny website. Version 14, July 2017 [and more or less continuously updated since]. http://www.mobot.org/MOBOT/research/APweb/ [accessed 28 January 2020]

Xu K, Shi X, Fan Q, Xu W, Liao W (2017) *Ilex calcicola* (Aquifoliaceae), a new species from a limestone area of Guangxi, China. *Phytotaxa* 326: 245–251. https://doi.org/10.11646/phytotaxa.326.4.2

Yao X, Song Y, Yang J, Tan Y, Corlett R (2021) Phylogeny and biogeography of the hollies (*Ilex* L., Aquifoliaceae). *Journal of Systematics and Evolution* 59: 73–82. https://doi.org/10.1111/jse.12567

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Grevillea merceri Olde & Marriott (Proteaceae: Grevilleoideae: Hakeinae) an uncommon, geographically isolated species in the *Triloba* Group from subcoastal areas of southern Western Australia

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Abstract

The existence of *Grevillea merceri* Olde & Marriott, herein described, was brought to light following a single collection by the late Ken Newbey in 1963. His specimen was treated by McGillivray and Makinson (1993: 187) as 'unassignable to species' but with possible affinity to *G. paniculata* Meisn., a species very broadly conceptualised in their work. Revision and a more restricted delimitation of *G. paniculata* by Olde & Marriott (1994, 1995) clarified the many significant differences from this specimen and others subsequently found. The relationship of *G. merceri* to other members of the *Triloba* Group however remains uncertain and awaits phylogenetic analysis.

Introduction

Members of the *Grevillea triloba* Group in Western Australia are distributed abundantly between Perth and Kalbarri and extend east to a line between the Fraser Range and Point Malcolm, just east of Cape Arid, at which distance they are infrequent and much less speciose. South of Perth relatively few species flourish, and some are narrowly endemic. Several days spent by the authors in search of *G. merceri,* combing the tracks around Boat Harbour, went unrewarded until its recollection during a plant survey by Mr Jack Mercer in 1996. Mercer's specimen was gathered on spongolite terraces, a porous stone made from fossilised sponges embedded with silica that formed probably during the Eocene when sea levels were much higher and sponges lived in the warm shallow sea. Several additional populations of *G. merceri* have been subsequently located. Botanist E.M. Sandiford located several populations between Boat Harbour and the Pallinup River with some of these on loamy soils in broad valleys. The new species appears to be geographically restricted.

Morphology

Descriptive layout and morphological terminology used in this and subsequent papers is outlined by Olde (2015). The transition from a Biological Species Concept to a Phylogenetic Concept will necessitate the

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recognition of more taxa at specific rank. Phylogenetically untested relationships should not, in the view of the authors, be embedded in the nomenclature and all morphological characters should be treated as equal, rather than hierarchically nested with some potentially trivialised at the expense of others.

Taxonomy

Grevillea merceri Olde & Marriott, **sp. nov.**

Type: Western Australia: Cheyne Bay Reserve, 151 m east of track to Jack's Beach, 5 Sep 2003, *N. Marriott NM03036, W. Renzi & J. Mercer* (holo: PERTH; iso: NSW 1100123, MEL) (*distribuendi*).

Grevillea Section *Manglesia* Unassignable to Species 'xviii' *sensu* McGillivray and Makinson (1993: 187).

Diagnosis: Related possibly to *Grevillea paniculata* Meisn. which differs in its narrower, ascending to spreading leaf lobes, with the abaxial surface tightly enclosed by the margin including at the sinuses, in its prominent nectary, in its conical pollen-presenter, in its sharply rugose fruits with high-walled ridges and verrucae.

Seedlings not seen. *Mature plants:* bushy, dark green, stenobasic, seed-obligate, apparently self-compatible *shrubs* 0.5–1.5 (–2) m high, 1–2 m wide, with lax, intricately tangled, downward-arching branches. *Branchlets* 1–2 mm thick, slender, angular when young, soon becoming terete, smooth, glabrous or rarely with scattered appressed short hairs, shiny. *New growth* tendril-like, rusty-sericeous, the hairs quickly evanescent. *Adult leaves* divided, 2–4 cm long, 3–7 cm wide, spreading to patent or slightly ascending, petiolate, 3–5-partite, with primary, secondary and occasionally tertiary orders of division, usually the lateral lobes secondarily bi- or tripartite, occasionally with tertiary tripartite division of one or both lateral lobes, the terminal lobe usually simple, elongate, sometimes bi- or tripartite, the lobes divaricate, frequently orthogonal; unimorphic, ovate in gross outline, crowded, frequently tangled, the rachis divaricately refracted; *primary leaf rachis* angularly refracted to ± orthogonal at each leaf node; segments straight; *basal internode* 9–25 mm long, 1 mm wide, unimorphous, parallel-sided, not alate, spreading at 45° from line of branchlet, straight, not reducing in length when subtending axillary growth, subterete-dipleural; the *adaxial surface* flat, glabrous; *abaxial surface* convex, glabrous; *primary lobes* 3–5, usually patent, sometimes ascending; *terminal lobes* usually simple, elongate, sometimes bi- or tripartite; *ultimate terminal lobes* (0.2–)1–3.5(–4.2) cm long, 1.2–1.7 mm wide, patent to spreading, sometimes descending, linear to acerose, straight or slightly curved, sometimes twisted, usually equal; *lateral lobes* usually secondarily bi- or tripartite, occasionally with tertiary tripartite division of one or both lateral lobes, sometimes retrorse, at each point of division the lobes orthogonal to the main axis; *ultimate lateral lobes* (0.2–)1–3.5(–4.2) cm long, 1.2–1.7 mm wide, patent to spreading, sometimes descending, linear to acerose, straight or slightly curved, sometimes twisted, usually equal; *apices of leaf lobes* acute to subulate, spinescent; *spine* 2–2.25 mm long, reddish amber with yellowish base, rigid, straight, pungent; *margins of lobes* angularly and vertically refracted about the intramarginal vein, almost abutting the midvein on the abaxial surface, enclosing most of the lamina except at the sinuses; *adaxial surface* flat, sometimes channelled beside midvein, glabrous or with a few scattered appressed hairs, smooth, not shiny, the midvein and intramarginal veins prominent; *abaxial surface* sometimes exposed at the sinuses, the epidermis not fully obscured by the margin, otherwise bisulcate, glabrous or with a few scattered hairs, the midvein glabrous, protuberant; *sulcae* 0.2–0.25 mm wide, white-sericeous; *texture* rigidly coriaceous. *petioles* 1–3 mm long, 1.5 mm wide, normal, 3–merous, spreading slightly at the point of attachment, the central segment developed down the branch, the lateral segments closely aligned, scar shape hemispherical; the adaxial surface slightly concave; the abaxial surface convex, glabrous. *Conflorescences* glabrous, terminal or subterminal, simple to 5-branched, secondary development lacking, clearly exceeding the leaves; *unit conflorescences* 1–1.5(–3.5) cm long, 1 cm wide, shortly cylindrical, 20–40 flowered, acropetal; *buds* 2 mm long, 0.6 mm wide, pedunculate, cylindrical to narrowly conico-cylindrical, pedunculate, not overarched by bractiform leaves, development not arrested; *peduncles* 5–10 mm long, glabrescent, slender; *floral rachises* 8–30 mm long, erect, straight, usually uniformly slender with slight distal taper, glabrous or with a few scattered appressed hairs; *rachis nodes* obscure, glabrous, the rim oblique; *involucral bracts* 1.25 mm long, *c.* 0.7 mm wide, ovate-apiculate, glabrous-ciliate, caducous at early bud stage; *common bracts* (subtending a single flower-pair) 0.5–0.8(–2) mm long, 0.5 mm wide, ovate, strongly inflected from *c.* half-way, reddish to rusty silky outside or sometimes glabrous with sparsely ciliate margins, variably caducous, most detaching as the bud develops but some persistent beyond anthesis. *Flower colour* white or pinkish-white with grey-green limb ageing reddish-cream. *Flowers* acroscopic, not nectariferous, slightly fragrant, entomophilous (pollinator unknown), glabrous; *pedicels* white, 7–11.5 mm long, 0.2–0.3 mm wide, filamentous, the apex below the torus scarcely expanded, spreading to ascending, straight to decurved, not crowded; *basal pedicels* white, 9–11.5 mm long; *distal pedicels* 7–9 mm long; *torus c.* 0.4 mm across, square in polar view, scarcely wider than pedicel apex, transverse to oblique at *c.*10°; *nectary* absent or obscure, white and rising *c.* 0.1 mm above the torus, crescentic, margin entire. *Pistils* 4–4.5 mm long; *gynophore* 1.5–3 mm

long; *ovary* 0.7 mm long 0.5 mm wide, round in side-view to slightly ovoid or ellipsoid with oblique base, slightly compressed laterally, not wrinkled after fertilisation; *style* constricted above ovary, then dilated; *stylar constriction* 0.1–0.3 mm long, 0.3 mm thick, incurved; *stylar swelling* 0.8 mm long, 0.7 mm maximum width, subcylindrical, abruptly dilated proximally, tapering slightly distally, sometimes then broadening slightly again below the style-end to 0.6 mm; *pollen-presenter* 0.6–0.7 mm long, truncate-conical to subcylindrical with straight to slightly incurved sides; *base* 0.7 mm wide, transverse to oblique at 10–20°, abruptly divergent from the style-end, rimmed; *stigma* 0.2 mm wide, transverse. *Perianth c.* 4 mm long, actinomorphic, *perianth tube* white, 2.5 mm long, 0.7–0.8 mm maximum width, narrowly obovoid, contracting below the limb into a neck 0.4–0.6 mm wide; *perianth limb* reddish-cream, 1.5 mm long 1.7 mm wide, subglobose with slight apical compression; *tepals* 4.5 mm long, 0.4 mm wide at base, 0.8 mm wide at widest point, 0.5 mm below the limb, abaxial surface with midrib prominent; adaxial surface smooth; *tepal-limbs* 1.2–1.5 mm long 1 mm wide, midrib prominent to obscure. *Follicles* 8–9 mm long, 5–5.5 mm wide, oblong-ellipsoidal, oblique on incurved gynophore with attachment subposterior, *c.* 1 mm from base; *fructual style* straight to decurved, attached obliquely to the dorsal side of the pericarp more or less lateral to the dorsal surface; *fructual pollen-presenter* truncate-conical to cylindrical; *pericarp* 0.4–0.5 mm thick along the suture, slightly thicker at the ends; exocarp smooth to slightly colliculose; *mesocarp* crustaceous; *endocarp* smooth. *Seeds* not seen. (Figures 1, 2)

Fig. 1. *Grevillea merceri*. A. Dense flowering branchlets and leaves. B. Flowering branchlet. C. Close-up of conflorescence. Photos by: A, Peter Olde; B, C, I. Gilmour.

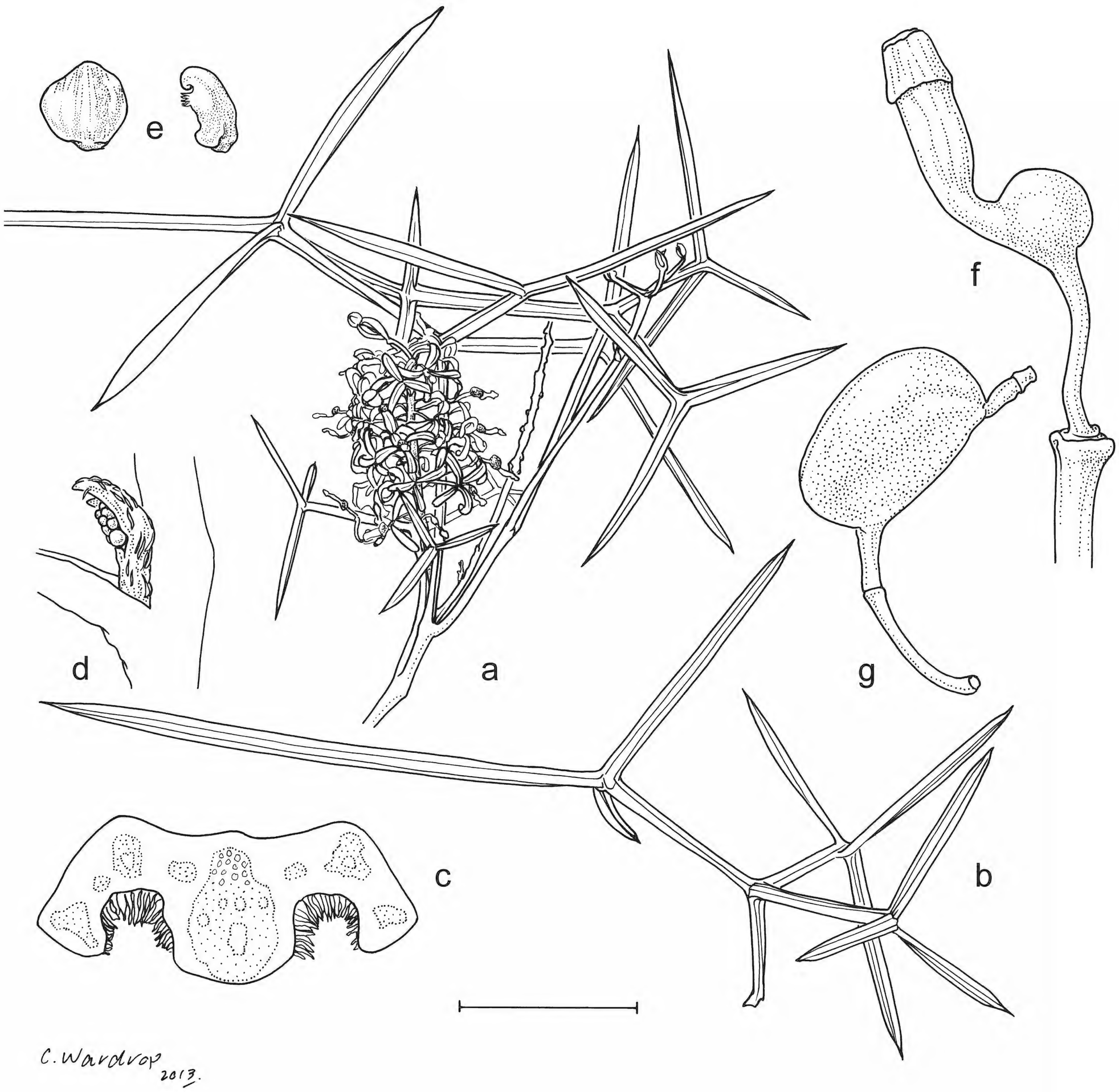

Fig. 2. *Grevillea merceri*. a. Flowering branch with an unbranched conflorescence. b. Leaf. c. Transverse section of leaf lobe. d. Unit conflorescence bud. e. Common bracts subtending flower pairs. f. Pistil. g. Follicle. Scale bar: a = 20 mm; b = 15 mm; c, d = 1 mm; f = 2 mm; g = 7.5 mm. Illustration by Catherine Wardrop from fresh and spirit material grown on Peter Olde's property.

Diagnostic characters: Stenobasic, seed-obligate, mostly glabrous shrub with spreading, tangled branchlets and foliage; leaves 3–5 partite often with orthogonal divarication and up to 3 orders of division; basal internode linear; ultimate leaf lobes > 1 mm wide, the abaxial surface not fully enclosed by the margins, the terminal lobe often elongate to 4 cm long; conflorescences terminal or subterminal, branched, pedunculate; buds narrowly conico-cylindrical; common bracts 0.5–0.8(–2) mm long, 0.5 mm wide, ovate, glabrous-ciliate, rarely sericeous on the abaxial surface; floral rachises 8–30 mm long, glabrous, the nodes obscure; nectary obscure; pollen-presenter 0.6–0.7 mm long, truncate-conical to subcylindrical; stigma 0.2 mm wide, fruits follicular, monospermous with smooth exocarp; mesocarp crustaceous; fructual style with pollen-presenter cylindrical or truncate-conical.

Distribution: Western Australia, south coast, from the Boxwood Hills area, east of Jerramungup and the Pallinup Valley to Boat Harbour. It occurs in the Fitzgerald Subregion of the Esperance Plains IBRA Region.

Phenology: Flowers from late winter through spring. Fruits form mainly from late spring.

Habitat and ecology: *Grevillea merceri* grows in yellowish sand or in rocky soil composed of laterite and spongolite and shallow pockets of fine brown sand, occurring on soils derived from the Tertiary Pallinup Formation. It occurs subcoastally on ridge tops at the edge of uneroded dykes or uncollapsed spongolite terraces

in low, open heathland with *Leptospermum* sp. Associated species recorded at one site include *Banksia media*, *Hakea marginata*, *H. nitida*, *H. pandanicarpa* ssp. *crassifolia*, *Kunzea pauciflora* and *Melaleuca violacea*. In the Lower Pallinup Valley, it grows with *Eucalyptus thamnoides* in Tall Mallee over Mixed Tall Open Shrubland with *Acacia leioderma*, *Hakea laurina, Melaleuca pentagona* and *Templetonia retusa*.

Conservation status: *Grevillea merceri* is known now from several populations within a geographically restricted area, although one population contains only 10 individuals. The species does not appear to be at all common in its preferred habitat. A suitable conservation code for Western Australia should be applied after populations have been assessed.

Etymology: This species is named after Jonathon 'Jack' William Mercer B.Sc. (Hons) (16 Apr 1953 –) who rediscovered this species during a plant survey and provided great help to the authors in relocating it for field assessment.

Variation: There is some minor variation in habit and flower colour. At Cheyne Beach a dense shrub with shortly arching branches and very showy rich brown flower buds, slowly becoming ontogenetically orange-yellow was observed. The second shrub had a more open starfish-shaped habit with long, arching branches and pale green-yellow buds becoming cream with development.

Discussion: McGillivray and Makinson (1993: 187) treated the taxon, here described as *Grevillea merceri,* as Section *Manglesia* Unassignable to Species 'xviii'. It was then known from a single collection (*Newbey* 809). They suggested a possible affinity with *G. paniculata* perhaps because of its glabrous branchlets and floral rachises. *Grevillea paniculata* differs in its leaf lobes narrower (0.5–0.8 mm wide), with ascending to spreading orientation, and with the abaxial surface tightly enclosed by the margin including at the sinuses, in its nectary prominent, rising up to 0.2 mm above the torus, in its pollen-presenter conical, in its fruits with a rugose exocarp with high-walled, sharp ridges and verrucae. The smooth fruits of *G. merceri* suggest a possible relationship with *G. levis* which differs in its usually rhizomatous habit, its narrower, spreading leaf lobes 0.5–0.8 mm wide, its prominent nectary and in its more prominent floral rachis nodes.

Specimens seen: WESTERN AUSTRALIA: Cheyne Bay Reserve, N of Cape Riche, 11 Oct 1996, *J.W. Mercer 179* (PERTH); Boat Harbour, 6 Aug 1963, *K. Newbey 809* (PERTH); Terraces adjacent to track leading to Jack's Beach, Boat Harbour, 27 Sep 2004, *P.M. Olde 04/281 & D. Shiells* (BRI, CANB, HO, K, MEL, NSW, PERTH); South Coast Highway, 6–6.5 km east of Circuit Rd., west of Swamp Rd., Wellstead, 16 Sep 2015, *P.M. Olde 15/225 & I. Evans* (NSW); 56 km from Jerramungup along road to Albany, 34°22'S 118°44'E, 28 Sep 1983, *R.W. Purdie 5424* (CBG); Lower Pallinup Valley, *c.* 750 m S of Pallinup River and 1.3 km WSW of Beaufort River, 6 Apr 2016, *E.M. Sandiford 2214* (PERTH).

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References

Marriott N (2005) Western Australia *Grevillea* research trip August–September 2003 Part 1. *Grevillea Study Group Newsletter* 70: 7–8. http://anpsa.org.au/grevSG/GSG-news.html

McGillivray DJ, Makinson RO (1993) Grevillea, *Proteaceae: a taxonomic revision*. (Melbourne University Press: Carlton, Victoria)

Olde PM (2015) *Grevillea laurifolia* subsp. *caleyana* Olde (Proteaceae: Grevilleoideae: Hakeinae), a new subspecies from the Blue Mountains of New South Wales, Australia. *Telopea* 18: 97–108. http://orcid.org/0000-0002-4333-0769

Olde PM, Marriott NR (1994) *The Grevillea Book, Volume 1*. (Kangaroo Press: Kenthurst, New South Wales)

Olde PM, Marriott NR (1995) *The Grevillea Book, Volume 3*. (Kangaroo Press: Kenthurst, New South Wales)

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The moss family Calymperaceae (Bryophyta) in Australia
Part 1: Introduction and key to genera

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Abstract

This paper is the first of five constituting a synopsis of the family Calymperaceae for Australia. An expanded concept of the family is followed, including *Arthrocormus*, *Exostratum* and *Leucophanes* as well as the traditional genera *Calymperes*, *Mitthyridium* and *Syrrhopodon*. A key to genera is provided.

Introduction

In its traditional sense, the moss family Calymperaceae Kindb. includes the genera *Calymperes* Sw., *Mitthyridium* (Mitt.) Robinson and *Syrrhopodon* Schwägr. (Reese and Stone 1995, 2012). A concise historical outline of the generic concepts of the traditional family with these three genera was provided by Reese *et al.* (1986a), and taxonomic relationships were later confirmed by molecular studies (Fisher *et al.* 2007; Stech *et al.* 2012).

In their treatment of Australian Calymperaceae, Reese and Stone (1995, 2012) noted that earlier authors, for example, Andrews (1947), had recommended that genera then assigned to Leucophanaceae: *Arthrocormus* Dozy & Molk., *Leucophanes* Brid. and *Octoblepharum* Hedw. should be included in the Calymperaceae. However, Reese and Stone (1995, 2012) preferred to maintain the traditional view. An expanded concept of the family, recognised by the Australian Moss Name Index (AusMoss 2020) based on Goffinet and Buck (2020), is followed in this updated treatment. This includes *Exostratum* L.T.Ellis, (1985) but excludes *Octoblepharum* Hedw., which is placed in its own family, Octoblepharaceae (Cairns *et al.* 2020), following Santos and Stech (2017a).

Calymperaceae as circumscribed here is a largely tropical and pantropical family. The family in Australia includes 50 species in six genera: *Arthrocormus* (1 sp.), *Calymperes* (15 spp.), *Exostratum* (1 sp.), *Leucophanes* (4 spp.), *Mitthyridium* (9 spp.), and *Syrrhopodon* (20 spp.).

As with other groups of organisms, Calymperaceae carries its own suite of descriptive terms for unique gametophyte characteristics. Terms used in this synopsis are based on their usage by earlier authors as cited, and in bryophyte glossaries (Buck 1990; Ramsay 2006; Malcolm and Malcolm 2006; Glime and Chavoutier 2017). These include:

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hyaline lamina (Fig. 1A): A region of transparent, lattice-like groups of **hyalocysts** in a single layer on each side of the costa, occupying the sheathing leaf base to variable extent. In older publications these groups of cells are often referred to as **cancellinae**.

hyalocysts (Fig. 1B): Large, empty, thin-walled, porose, usually colourless water-storage cells. Hyalocysts are dead at maturity, in contrast to **hyaline cells** which may retain their cell contents but are colourless due to the absence of chloroplasts. The term **leucocyst** (as occur in the Leucobryaceae) is considered to be a synonym but molecular analyses (e.g., Santos and Stech 2017b, Fisher *et al.* 2007) showed the leucobryoid genera in Calymperaceae (and Octoblepharaceae) to not be closely related to those in the Leucobryaceae; cells are morphologically similar but not homologous. We have chosen to use **hyalocyst** in descriptions of Calymperaceae taxa throughout this series. Hyalocysts in the hyaline lamina are occasionally called **endohyalocysts**, a term we consider unnecessary.

chlorocysts (chlorophyllose cells): Cells containing chlorophyll, green in fresh material. At least for *Arthrocormus* and *Exodictyon*, the arrangement of the chlorophyllous cells, both in section and in surface view of the leaf limb, is important in generic identification.

intramarginal cells (Fig. 1C): Many *Calymperes* species have leaves with a narrow strip of elongate, often thick-walled, hyaline **intramarginal cells** in 1–4(–6) rows, widest at shoulders, and generally 1–2(–4) cells thick. These may be weak, obscure, or lacking in some leaves. In older publications these thickenings are often referred to as **teniolae**. A unistratose extension of the intramarginal cells into the sheathing leaf base, referred to in older publications as a **parateniola**, may also be present in some *Calymperes* species, for example, *C. erosum* (Edwards 1980a). Recent publications simplify terminology and include all intramarginal cells in the 'intramarginal rib' (Ellis 2018, 2020).

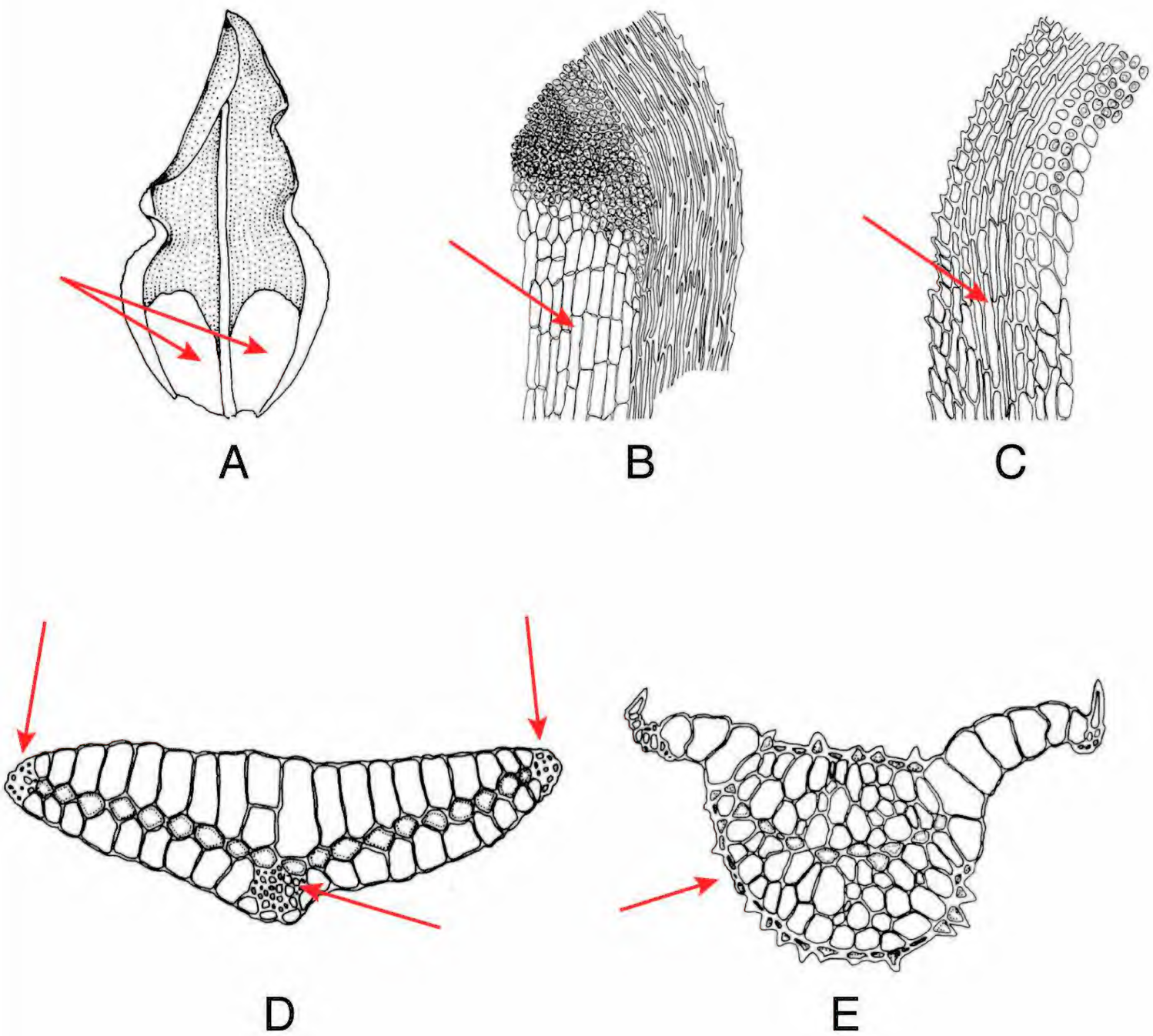

Fig. 1. Characteristics of the gametophyte of Calymperaceae. **A** hyaline lamina (*Mitthyridum repens*). **B** hyalocysts (*Mitthyridium repens*). **C** intramarginal cells (*Calymperes moluccense*). **D** marginal stereomes and medial stereome (*Leucophanes octoblepharoides*). **E** leucobryoid costa (*Exostratum blumei*). Illustrations by R.D. Seppelt.

stereome (Fig. 1D): Supporting or strengthening tissue; for example, the thickened marginal border of some taxa, which may include narrow elongate and thick-walled cells surrounded by the lamina cells of the border (**marginal stereome**). In *Leucophanes* a **medial stereome** comprised of stereids is a significant character of the genus, variously termed 'median strand', 'median stereome' or 'pseudonerve' by Eddy (1990), 'central stereid

band' by Enroth (1990), and 'pseudocosta' by Catcheside (2012). Descriptions of *Leucophanes* species in Part 2 of this synopsis will refer only to the **medial stereome**.

leucobryoid costa (Fig. 1E): The leaf structure of the leucobryoid genera *Arthrocormus, Exodictyon* (not yet reported from Australia), *Exostratum*, and *Leucophanes*, has been interpreted in various ways, beginning with Cardot (1900). Termed 'pseudolamina' (Eddy 1990; Catcheside 2012), leaves of these genera 'consist mainly of a very wide costa composed of two to several layers of large hyaline cells (leucocysts or hyalocysts) surrounding one (or up to three) layer(s) of chlorophyllose cells (chlorocysts)' (Santos and Stech 2017b), with a 'hyaline lamina restricted to the lowest parts of the leaves' (Eddy 1990). This is the structure most commonly recognised in descriptions of the leucobryoid genera.

CALYMPERACEAE Kindb., *Gen. Eur. N.-Amer. Bryin.*: 11 (1897)

Type genus: Calymperes Sw. ex F.Weber

Plants acrocarpous, tufted, with erect simple or branched stems (in *Mitthyridium*, primary stems are creeping), mainly small and less than 4 cm tall, occasionally robust to 6 cm or more and with leaves over 1 cm long. Stems without a central strand; rhizoids usually reddish or brown. Leaves diverse in form, costate, most commonly with a differentiated row of cells forming a border or (in *Calymperes*) intramarginal, with a conspicuously differentiated and usually abruptly delineated hyaline lamina; leaf outline typically linear but commonly ligulate or spathulate; leaf apex variable, sometimes expanded and modified to form a receptacle enclosing a gemmiferous zone, gemmiferous leaves often differing morphologically from stem leaves. Costa usually strong, typically of 2–6 median guide cells in a single row (sometimes with additional guide cells not in a row), adaxial and abaxial stereid bands, and a differentiated epidermal layer; strongly modified and composed largely of hyalocysts and superficial chlorocysts (in *Arthrocormus, Exostratum, Leucophanes*); costa variously excurrent, percurrent, or ending below leaf apex, often with scattered or localised regions bearing fusiform, multicellular gemmae. Dioicous. Perigonia and perigynia terminal on unmodified shoots; perichaetia usually inconspicuous, perichaetial leaves similar to normal leaves or the innermost reduced. Sporophytes relatively small; capsules cylindrical or ovoid-cylindrical; setae of variable length. Calyptra variable, small or large, sometimes conspicuously plicate. Peristome simple, of 16 narrow, papillose segments (lacking in *Calymperes*).

The above description is modified from Eddy (1990) and differs from the family description of Reese and Stone (2012), taking into consideration the broader family concept followed here.

Of the non-leucobryoid genera now included in the family, the genus *Calymperes* is most closely related to *Syrrhopodon*. A critical distinguishing feature is the presence in *Calymperes* of a persistent calyptra which may play a peristome-like role in regulating spore dispersal (Edwards 1980b). In *Syrrhopodon* the calyptra is shed prior to spore dispersal. The differentiated leaf margin found in many species of Calymperaceae is also often useful in separating *Calymperes* from *Syrrhopodon*. In *Syrrhopodon*, when present the sheathing base is often marginally bordered and only rarely is the extension of this intramarginal.

Mitthyridium is the only genus present having prostrate primary stems with erect branches.

Regional floras and specific generic or family treatments which provide much useful additional information relevant to the Calymperaceae recorded from Australia and neighbouring regions include:

Australia — Ellis (2003); Reese (1989, 1992); Reese and Stone (1987, 1995, 2012);

India — Ellis (1989, 2016a);

Malaysia — Ellis (2016b); Reese *et al.* (1986b); Reese and Mohamed (1985); Tixier (1978);

Malesia (including the Philippines, Papua New Guinea): Akiyama and Reese (1992); Eddy (1990); Ellis (1991, 2020), Ellis and Tan (1999); Menzel and Schultze-Motel (1990); Mohamed and Reese (1985);

Oceania — Nowak (1980);

Thailand — Promma and Chantanaorrapint (2013);

World-wide (*Calymperes*) — Reese (1987).

In the following key to genera of Australian Calymperaceae, *Exodictyon* Card. (although not yet reported from Australia) is included for completeness and to enable ready differentiation from the one species of the genus *Exostratum* that is known from Queensland.

Key to the genera of Calymperaceae in Australia

1 Leaves whitish green, consisting almost entirely of costa composed of hyalocysts, and 1–3 strata of green chlorocysts; true lamina composed only of hyaline cells with a narrow border of elongate, thick-walled cells 2

1: Leaves yellow-green, green, brownish-green, not whitish, consisting of a well-defined lamina and costa; hyalocysts confined to the hyaline lamina 5

2 In section, costal chlorocysts arranged in a single medial layer ..... *Leucophanes*

2: In section, costal chlorocysts arranged in three layers, adaxial, medial and abaxial 3

3 Leaves very fragile, the distal portions commonly missing; in section, peripheral chlorophyllous layers covered by one layer of hyalocysts ..... *Arthrocormus*

3: Leaves not or hardly fragile, the distal portions mostly intact; in section, costal chlorocysts somewhat exposed at surface 4

4 In section, costal surface composed of a continuous layer of chlorocysts, many with spinulose or coronate-papillose projections; in surface view most chlorocysts quadrate to shortly rectangular or elliptical ..... *Exostratum*

4: In section, costa surface composed of hyalocysts and a reticulate network of chlorocysts; chlorocysts smooth or with low papillae, rarely with conspicuous projections, mostly with 4–6 sides in surface view ..... *Exodictyon*

5 Plants bearing sporophytes 6

5: Plants lacking sporophytes 8

6 Calyptra persistent, spirally furrowed when dry, twisted round the seta below the capsule, opening above by slit-like apertures; peristome lacking ..... *Calymperes*

6: Calyptra cucullate, deciduous; peristome present or absent; or calyptra not present 7

7 Stems usually creeping, often rhizome-like, with ascending-erect branches; leaves bordered (often broadly so) by elongate hyaline cells, the border unistratose ..... *Mitthyridium*

7: Stems erect, neither creeping nor rhizome-like, simple or forked; border of elongate hyaline cells present or absent, if present then narrow and bi- to multistratose ..... *Syrrhopodon*

8 Leaves bordered entirely or in part by elongate hyaline cells (border weak, incomplete or ± lacking on some leaves of some specimens) 9

8: Leaves lacking elongate hyaline marginal cells 11

9 Stems usually creeping, often rhizome-like, with spreading erect branches; border of hyaline cells on leaves often broad, always unistratose ..... *Mitthyridium*

9: Stems mostly erect, neither repent nor rhizome-like, simple or forked; border of hyaline cells narrow, mostly bi- to multistratose 10

10 Plants very small; leaves strongly dimorphic; gemmiferous leaves narrow, stiffly erect, almost elaminate; border of hyaline cells incomplete, unistratose, often present only near leaf shoulders ..... *Calymperes (subintegrum)*

10: Plants small to robust; leaves ± monomorphic; border of hyaline cells mostly well-developed, usually bi- to multistratose ..... *Syrrhopodon*

11 Leaves bearing intramarginal rows of differentiated elongate mostly hyaline cells; intramarginal cells sometimes indistinct or obscured or ± lacking in some leaves of some specimens ..... *Calymperes*

11: Leaves lacking intramarginal rows of elongate hyaline cells 12

12 Plants very small to medium-sized, commonly bearing abundant fusiform uniseriate-multicellular gemmae on modified tips of gemmiferous leaves; gemmiferous leaves often strongly differentiated from vegetative leaves and almost always present even though gemmae may have been lost 13

12: Plants medium-sized to robust; gemmae mostly lacking or inconspicuous; gemmiferous leaves, if present, not markedly different from vegetative leaves 14

13 Rhizoids dark red ..... *Syrrhopodon* (*stoneae*)

13: Rhizoids brown to reddish-brown ..... *Calymperes*

14 Cells of leaf limb ± transversely elongate, at least in part ..... *Calymperes*

14: Cells of leaf limb isodiametric to somewhat vertically elongate ..... *Syrrhopodon*

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References

Akiyama H, Reese WD (1992) Taxonomic studies of mosses of Seram and Ambon (Moluccas, East Malesia) collected by Indonesian-Japanese botanical expeditions. VI. Calymperaceae. *Acta Phytotaxonomica et Geobotanica* 43: 111–119.

Andrews AL (1947) Taxonomic notes VI. The Leucobryaceae. *The Bryologist* 50: 319–326. https://doi.org/10.1639/0007-2745(1947)50[319:TNVTL]2.0.CO;2

AusMoss (2020) Australian Moss Names Index. https://moss.biodiversity.org.au/nsl/services/search/names (accessed 3 October 2020)

Buck WR (1990) Glossarium polyglottum bryologiae: A multilingual glossary for bryology. Edited by RE Magill. *Monographs in Systematic Botany from the Missouri Botanical Garden* 33: 1–297.

Cairns A, Meagher D, Seppelt RD, Franks AJ (2020) The moss family Octoblepharaceae A.Eddy ex M.Menzel in Australia. *Telopea* 23: 237–244. http://dx.doi.org/10.7751/telopea14820

Cardot J (1900) Recherches anatomiques sur les Leucobryaceés. *Mémoires de la Société nationale des sciences naturelles et mathématiques de Cherbourg* 32: 1–84. https://www.biodiversitylibrary.org/item/44819#page/11/mode/1up

Catcheside DG (2012) Australian Mosses Online. 13. Calymperaceae: *Leucophanes*. http://www.anbg.gov.au/abrs/Mosses_online/12_Calymperaceae/Calymperaceae_Leucophanes.pdf (accessed 20 February 2021)

Eddy A (1990) *A handbook of Malesian mosses. Vol. 2. Leucobryaceae to Buxbaumiaceae*. Natural History Museum Publications, London.

Edwards SR (1980a) A revision of West Tropical African Calymperaceae I. Introduction and *Calymperes*. *Journal of Bryology* 11: 49–93. https://doi.org/10.1179/jbr.1980.11.1.49

Edwards SR (1980b) Spore discharge in *Calymperes*. *Journal of Bryology* 11: 95–97. https://doi.org/10.1179/jbr.1980.11.1.95

Ellis LT (1989) A taxonomic revision of *Calymperes* in southern India and neighbouring islands. *Journal of Bryology* 15: 697–732. https://doi.org/10.1179/jbr.1989.15.4.697

Ellis LT (1991) *Calymperes schmidtii* Broth. *in* J. Schmidt and *C. subintegrum* Broth. *in* J. Schmidt, two distinct species from Malesia. *Journal of Bryology* 16: 589–593. https://doi.org/10.1179/jbr.1991.16.4.589

Ellis LT (2003) A revised synonymy for *Syrrhopodon trachyphyllus* (Calymperaceae, Musci) and some related Old World taxa. *Systematics and Biodiversity* 1: 159–172. https://doi.org/10.1017/S1477200003001154

Ellis LT (2016a) *Syrrhopodon* Schwägr. (Calymperaceae, Musci) in India and adjacent regions. *Journal of Bryology* 38: 1–27. https://doi.org/10.1179/1743282015Y.0000000024

Ellis LT (2016b) A new species of *Syrrhopodon* (Calymperaceae) from Sarawak. *Journal of Bryology* 38: 259–262. https://doi.org/10.1080/03736687.2015.1115617

Ellis LT (2018) Taxonomic notes on *Calymperes erosum* Müll.Hal. (Calymperaceae), *C. palisotii* Schwägr. and related West African taxa. *Journal of Bryology* 40: 333–341. https://doi.org/10.1080/03736687.2018.1478652

Ellis LT (2020) Notes on *Calymperes* subg. *Calymperes* (Calymperaceae) in the Malesian-Pacific region, with special reference to *C. subulatum* E.B.Bartram, *C. beccarii* Hampe and a new species from Borneo. *Journal of Bryology* 42: 301–315. https://doi.org/10.1080/03736687.2020.1824880

Ellis LT, Tan BC (1999) The moss family Calymperaceae (Musci) in the Philippines. *Bulletin of the Natural History Museum. Botany series. London* 29: 1–46. https://www.biodiversitylibrary.org/item/19420#page/3/mode/1up

Fisher KM, Wall DP, Yip KL, Mishler BD (2007) Phylogeny of the Calymperaceae with a rank-free systematic treatment. *The Bryologist* 110: 46–73. https://doi.org/10.1639/0007-2745(2007)110[46:POTCWA]2.0.CO;2

Goffinet B, Buck WR (2020) Classification of the Bryophyta. http://bryology.uconn.edu/classification/ (accessed 5 September 2020)

Glime JM, Chavoutier L (2017) Glossary. In: Glime JM (ed.) *Bryophyte Ecology*. Ebook sponsored by Michigan Technological G-1 University and the International Association of Bryologists. http://digitalcommons.mtu.edu/bryophyte-ecology/ (accessed 2 March 2021)

Malcolm W, Malcolm N (2006) *Mosses and other bryophytes, an illustrated glossary.* Micro-Optics Press, Nelson, New Zealand.

Menzel M, Schultze-Motel W (1990) The bryophytes of Sabah (North Borneo) with special reference to the BRYOTROP transect of Mount Kinabalu. XI Calymperaceae (Bryopdsida). *Willdenowia* 19: 475–542. https://www.jstor.org/stable/3996656

Mohamed H, Reese WD (1985) *Syrrhopodon* (Musci: Calymperaceae) in Malaysia and adjacent regions. *The Bryologist* 88: 223–254. https://doi.org/10.2307/3243033

Nowak H (1980) Revision der Laubmoosgattung *Mitthyridium* (Mitten) Robinson für Ozeanien (Calymperaceae). *Bryophytorum Bibliotheca* 20: 1–236.

Promma C, Chantanaorrapint S (2013) The genus *Leucophanes* (Calymperaceae, Bryophyta) in Thailand. *Thai Forest Bulletin (Botany)* 41: 23–38. https://li01.tci-thaijo.org/index.php/ThaiForestBulletin/article/view/24096

Ramsay H (2006) Glossary. In *Flora of Australia Vol. 51 Mosses 1*: 413–429. ABRS Canberra and CSIRO Publishing Melbourne.

Reese WD (1987) *Calymperes* (Musci: Calymperaceae): world ranges, implications for patterns of historical dispersion and speciation, and comments on phylogeny. *Brittonia* 39: 225–237. https://doi.org/10.2307/2807380

Reese WD (1989) Two new taxa of *Syrrhopodon* (Musci: Calymperaaceae) from Australia. *The Bryologist* 92: 302–304. https://doi.org/10.2307/3243396

Reese WD (1992) *Syrrhopodon cyrtacanthos*, a new species of moss from Australia. *The Bryologist* 95: 94–96. https://doi.org/10.2307/3243791

Reese WD, Koponen T, Norris DH (1986a) Bryophyte flora of the Huon Peninsula, Papua New Guinea. XIX. *Calymperes, Syrrhopodon* and *Mitthyridium* (Calymperes, Musci). *Acta Botanica Fennica* 133: 151–202.

Reese WD, Mohamed H (1985). A synopsis of *Calymperes* (Musci: Calymperaceae) in Malaysia and adjacent regions. *The Bryologist* 88: 98–109. https://doi.org/10.2307/3242588

Reese WD, Mohamed H, Mohamed DA (1986b) A synopsis of *Mitthyridium* (Musci: Calymperaceae) in Malaysia and adjacent regions. *The Bryologist* 89: 49–58. https://doi.org/10.2307/3243077

Reese WD, Stone IG (1987) New records of Australian Calymperaceae and keys to Australian species of *Calymperes, Mitthyridium,* and *Syrrhopodon*. *Journal of Bryology* 14: 487–493. https://doi.org/10.1179/jbr.1987.14.3.487

Reese WD, Stone IG (1995) The Calymperaceae of Australia. *Journal of the Hattori Botanical Laboratory* 78: 1–40. https://doi.org/10.18968/jhbl.78.0_1

Reese WD, Stone IG (2012) Australian Mosses Online. 13. Calymperaceae. http://www.anbg.gov.au/abrs/Mosses_Online/Calymperaceae_family.pdf (accessed 20 September 2020)

Salazar Allen N (1993) A revision of the pantropical moss genus *Leucophanes* Brid. *Bryophytorum Bibliotheca* 46: 1–281.

Santos MB, Stech M (2017a) Tackling relationships and species circumscriptions of *Octoblepharum*, an enigmatic genus of haplolepideous mosses (Dicranidae, Bryophyta). *Systematics and Biodiversity* 15: 16–24. https://doi.org/10.1080/14772000.2016.1213325

Santos MB, Stech M (2017b) Testing hypotheses on suprageneric relationships and morphological evolution in the Leucobryaceae (Bryophyta). *Plant Systematics and Evolution* 303: 1383–1397. https://doi.org/10.1007/s00606-017-1459-y

Stech M, McDaniel SF, Hernández-Maqueda R, Ros-Espín RM, Werner O, Muñoz J, and Quandt D (2012) Phylogeny of haplolepideous mosses – challenges and perspectives. *Journal of Bryology* 34: 173–186. https://doi.org/10.1179/1743282012Y.0000000014

Tixier P (1978) Le genre *Syrrhopodon* Schwägr. (Calymperaceae) en Indo Malaisie. *Nova Hedwigia* 29: 957–1023.

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The moss family Calymperaceae (Bryophyta) in Australia. Part 2: The genera *Arthrocormus*, *Exostratum* and *Leucophanes*

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Abstract

This is the second in a five-part series of papers that constitute a synopsis of the family Calymperaceae for Australia. It treats the genera *Arthrocormus* (one species), *Exostratum* (one species) and *Leucophanes* (four species) and includes detailed descriptions and illustrations of each species, critical identification features, notes on similar species, and distribution maps.

Introduction

One species of *Arthrocormus*, one species of *Exostratum* and four species of *Leucophanes* have been recorded from Australia. Enroth (1990) enumerated an additional two species of *Exostratum* and one species of *Leucophanes* from Papua New Guinea, but these have not been reported from Australia despite the proximity of the two land masses and the presence of land bridges during various past geological periods of lower sea level. However, much of the moss flora of tropical and subtropical Australia (the northern part of Western Australia, Northern Territory and Queensland) remains largely under-collected.

The following descriptions of species are based on our study of specimens held in Australian herbaria and our own collections, our observations in the field, and previous descriptions in Ellis (1985), Eddy (1990), Enroth (1990), and Catcheside (2012a, 2012b, 2012c). The notation !d indicates that a high-resolution digital image of a specimen has been seen via JSTOR Global Plants (plants.jstor.org).

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Taxonomic Treatment

ARTHROCORMUS Dozy & Molk., *Musci frond. ined. Archip. indici*: 76 (1846).

Type: ***Arthrocormus schimperi*** (Dozy & Molk.) Dozy & Molk.

A monotypic genus. Leaves consisting mainly of a hyaline costa with medial and peripheral chlorocyst layers. Lamina composed only of hyaline cells with a distinct narrow border of narrow elongate thick-walled cells. Dioicous. Fruiting plants rare.

Etymology: Greek *arthros* (jointed) + *kormos* (stem), referring to the jointed appearance of the branches.

1. *Arthrocormus schimperi* (Dozy & Molk.) Dozy & Molk., *Musci frond. ined. Archip. indici*: 76 (1846).

Basionym: *Mielichhoferia schimperi* Dozy & Molk., *Ann. Sci. Nat., Bot.*, sér 3(2): 312 (1844), *non* Besch. (1897).

Original material: 'Borneo'.

Type: Indonesia: Kalimantan, Martapoera, *P.W.Korthals s.n.*, 1831–1836 (possible holo L 0623687, *fide* Dozy. & Molk., 1846: 75).

Note: Although not stated in the protologue for the species, Korthals was cited as the collector when Dozy and Molkenboer (1846: 75) transferred it to *Arthrocormus*. He was in the Dutch East Indies between 1831 and 1837 (Stafleu and Cowan 1979: 651). The Indonesian state of Kalimantan is the only area of Borneo that was part of the Dutch East Indies. The location is taken from Touw (2013).

Illustrations: Fig. 1. Also: Eddy (1990: 34, fig. 187).

Description: Plants forming low tufts to 2 cm tall, simple, or sparingly branched, whitish green, when dry often tinged with brown, glossy; with dark brown rhizoids below; stems in section rounded triangular, without a central strand. Leaves consisting mainly of costa, to 5–6 mm in length, crowded, brittle, erect-spreading wet or dry, indistinctly tristichous, linear from a narrow concave hyaline sheathing base abruptly narrowed to an acute apex (the apex often broken off); margins entire below, ± denticulate above; costa ± rounded-trigonous in section, composed mainly of thin-walled hyalocysts with medial and peripheral layers of chlorocysts, the chlorocysts polygonal in section; hyaline cells of lamina confined to sheathing base of leaf, of 6–8 rows of large thin-walled hyalocysts and unistratose border 2–5 cells wide of thick-walled linear, stereid-like cells. Dioicous, fruit apparently rare. Seta slender, 6–8 mm long. Capsule erect, symmetrical, ovoid-cylindrical, urn 1–1.25 mm long. Peristome easily broken, of 16 simple, papillose teeth.

Etymology: After bryologist Wilhelm Philippe Schimper (1808–1880).

Distribution: *Arthrocormus schimperi* is known in Australia from several localities in north-eastern Queensland, from the Torres Strait islands to Tully (Fig. 7.1).

Habitat: Corticolous on tree trunks. Elsewhere widespread throughout tropical Asia from Sri Lanka, Thailand to Malesia, Sabah, the Philippines, Papua New Guinea, Torres Strait islands, Fiji, Samoa, Society Islands. Ellis (2002) noted that the species was often a common component of the corticolous moss communities throughout its Indo-Pacific range, especially in lowland tropical rainforest.

Recognition: The leaves are fragile and often broken. Eddy (1990) states that "… due to the extreme fragility of its leaves, botanists have a tendency to pass over plants in the field as damaged specimens of this or some other 'leucobryoid' moss." Leaf fragments are presumably the principal means of dispersal.

Arthrocormus is easily distinguished from *Octoblepharum albidum* (family Octoblepharaceae), a pantropical leucobryoid moss (Cairns *et al.* 2020), by its bordered and sheathing leaf base and the leaf section showing three layers of chlorocysts. Both *Exodictyon*, so far not yet recorded from Australia, and *Exostratum* have similar leaf sectional anatomy but differ in the form of the leaf margin, the leaf limb appearing rough or hispid due to the papillosity of the chlorocyst external walls. The superficial chlorocysts of *Exodictyon* form a unique network of cells, not found in *Exostratum*. *Exodictyon* extends into islands of the Southern Pacific with *E. dentatum* recorded from New Caledonia, east to Tahiti in the Society Islands, and *E. incrassatum* known from Papua New Guinea, the Solomon Islands and Samoa (Ellis 1985; Enroth 1990). It is possible that the genus may be found in northern Australia.

Selected specimens seen: Queensland: Torres Strait: Moa Island, Banks (Moa) Peak, *D.G.Fell, J.Wigness, I.Marass, F.Wapau DGF MP 91*, 17 Nov 2017, BRI AQ1002555; Queensland: Cook District; Cape Tribulation. Myall Creek, lowland riparian rainforest, *D.A.Meagher and A.Cairns WT-176,* 12 May 2013, BRI AQ1016927.

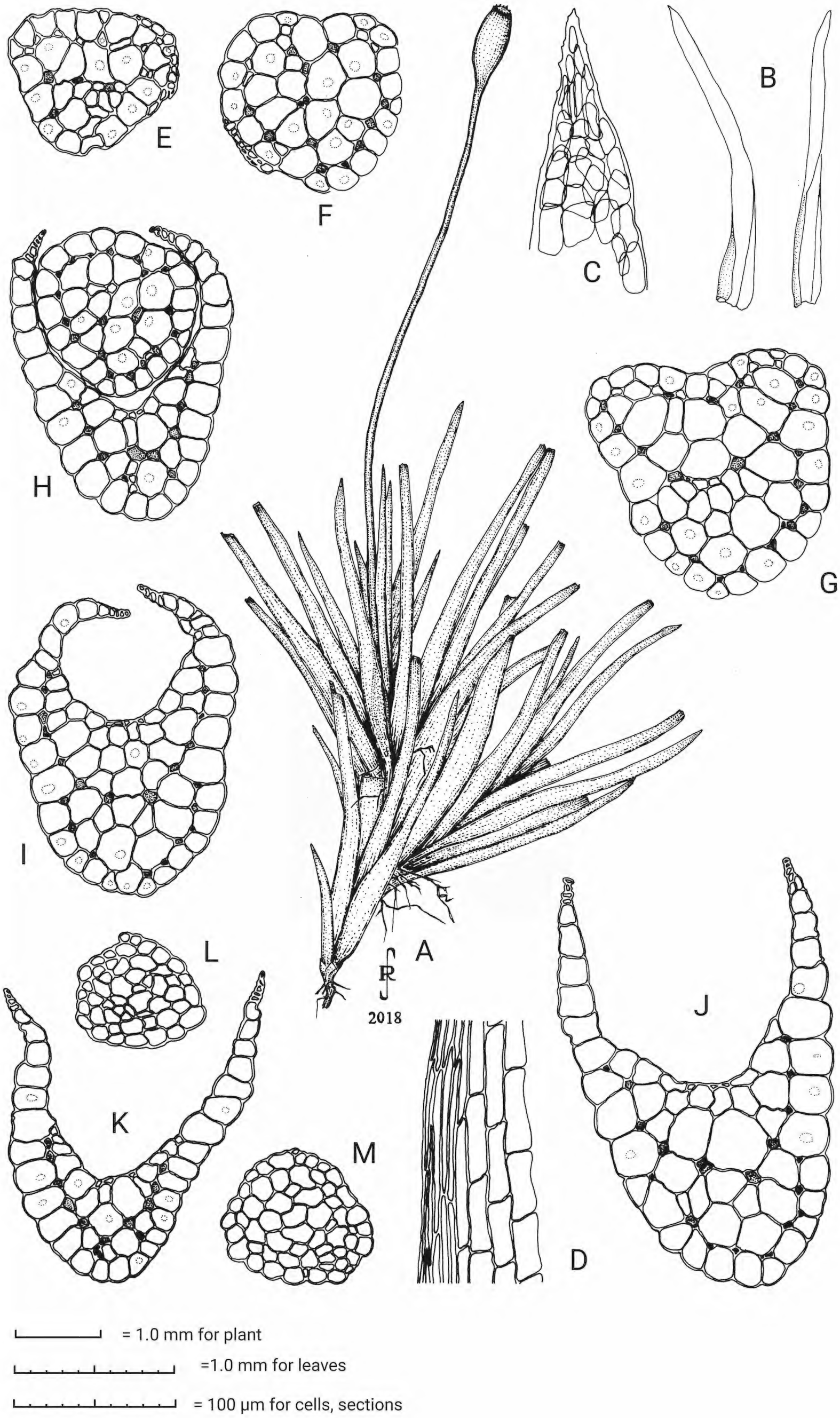

Fig. 1. *Arthrocormus schimperi* (Dozy & Molk.) Dozy & Molk. **A:** Habit of fruiting plant, drawn moist. **B:** Stem leaves. **C:** Cells of leaf apex. **D:** Marginal cells of sheathing leaf base. **E–G:** Sections of leaf blade. **H:** Section of clasping leaf base with included costal section of accompanying leaf. **I–K:** Sections of basal sheathing part of leaf. **L, M:** Stem sections. Drawn from: *D.G.Fell, J.Wigness, I.Marass, F.Wapau DGF MP 91* (BRI).

EXOSTRATUM L.T.Ellis, *Lindbergia* 11(1): 22 (1985).

Type: *Exostratum blumei* (Nees ex Hampe) L.T.Ellis

Description: Plants slender, forming whitish-green tufts, cushions or mats. Stems red, erect, slender, sparsely to abundantly branched; central strand lacking. Leaves in three regular or obscure ranks, with a reflexed to squarrose subula from a hyaline sheathing base, the subula often twisted; leaves little altered when dry. Costa filling subula, with 4–8(–9) layers of hyalocysts and 3 layers of small chlorocysts (adaxial, abaxial, medial) in transverse section; surface chlorocyst layers of subula continuous, epidermal surface with spiniform or coronate projections. Hyaline lamina unistratose, several cells wide in leaf base, abruptly to gradually narrowing into subula, ceasing just below or reaching apex. Rhizoids abundant at base of stem and branches, sometimes also arising from leaf apices. Gemmae in clusters at leaf tips, clavate to fusiform. Dioicous. Gametangia terminal. Seta red, spirally twisted, smooth. Operculum conical long rostrate. Annulus present. Peristome single, 16 teeth in 8 pairs, outer surface with papillose ridges. Spores finely papillose. Calyptra mitriform.

Etymology: Greek *exos* (outside) + Latin *stratum* (layer), referring to the continuous layers of chlorocysts over the supporting hyalocysts in the leaves.

Note: A genus related to (and once included in) *Exodictyon* Card., from which it differs in having the superficial chlorocysts forming a more-or-less continuous unistratose layer over both adaxial and abaxial surfaces of the costa (Ellis 1985: 18, fig. 4). Ellis (1985) recognised four species in *Exostratum*, of which only *E. blumei*, the type species of the genus, is currently known from Australia.

2. *Exostratum blumei* (Nees ex Hampe) L.T.Ellis, *Lindbergia* 11(1): 25 (1985).

Basionym: *Syrrhopodon blumii* Nees ex Hampe, *Bot. Zeitung* (*Berlin*) 5: 921 (1847).

Original material: none cited.

Type (not cited by Hampe): Indonesia: Java, *Blume s.n., n.d.* ex herb. Nees H.1226 p.p. (holo (*fide* Ellis in annot.) BM000665434!d; iso BM000665432!d, BM000665433!d, BM000665428!d, BM000665377!d, NY01140352!d (*fide* Ellis 1985), L0060226 not seen.

Note: Ellis (1985: 25) nominated a lectotype in citing 'Type specimen: Java, C. L. Blume s. n., in Herb. A. Braun, formerly in Herb. Nees (holotype formerly in B, destroyed 1943; lectotype L – designated here; isotypes BM, NY).' However, the holotype is extant (BM000665434, herb. Hampe) and is annotated as such by Ellis. The designation of a lectotype was therefore unnecessary, and other segregates identified with the number H.1226 as noted above are isotypes.

Illustrations: Fig. 2. Also: Ellis (1985: 26, fig. 10; 27, fig. 11; 28, fig. 12); Eddy (1990: 38, fig. 189).

Description: Plants slender, reaching to more than 3 cm high. Leaves 3–4 mm long, about 0.2 mm wide in mid-limb, long, narrow subulate, acute to subacute, dentate. In section, chlorocysts in 3 layers, adaxial, abaxial and medial, the outer walls of outer layers with anteriorly directed spiniform projections. Hyaline lamina in subula 0–1(–2) cells wide on each side of costa; margins of lamina around leaf shoulders often recurved. Gemmae frequently produced, linear, of few to many ± quadrate cells.

Etymology: After German–Dutch bryologist Carl Ludwig von Blume (1796–1872), who collected the type.

Distribution: *Exostratum blumei* occurs in north-eastern Queensland, from north of Cape Tribulation to Tully (Fig. 7.2). Also known in tropical Asia from southern India, Sri Lanka, south east Asia, China, Taiwan, southern Japan islands, Vietnam, Malesia, the Philippines, New Caledonia, Solomon Islands, Fiji, and Samoan islands. Throughout its range, the species is highly variable.

Habitat: Grows on tree trunks, branches, exposed roots of living trees including palms, logs, decaying wood, rarely on rock. Ellis (1985) noted that the species grew in shady places from 100–1700 m above sea level.

Recognition: Both *Exodictyon*, so far not yet recorded from Australia, and *Exostratum* have similar leaf sectional anatomy but differ in the form of the leaf margin: the leaf limb of *Exostratum* appearing rough or hispid due to the papillosity of the chlorocyst external walls. The superficial chlorocysts of *Exodictyon* form a unique network of cells, not found in *Exostratum*.

Selected specimens seen: Queensland: Lacey's Creek turn off from El Arish-Mission Beach Road, on roots near car park, *D.A.Meagher and A.Cairns WT–540,* 25 Nov 2014, BRI AQ1020936; Cassowary Coast, El Arish State Forest, *I.G.Stone 20080*, 11 July 1982 (ex MEL 2246588, as BRI AQ0874614).

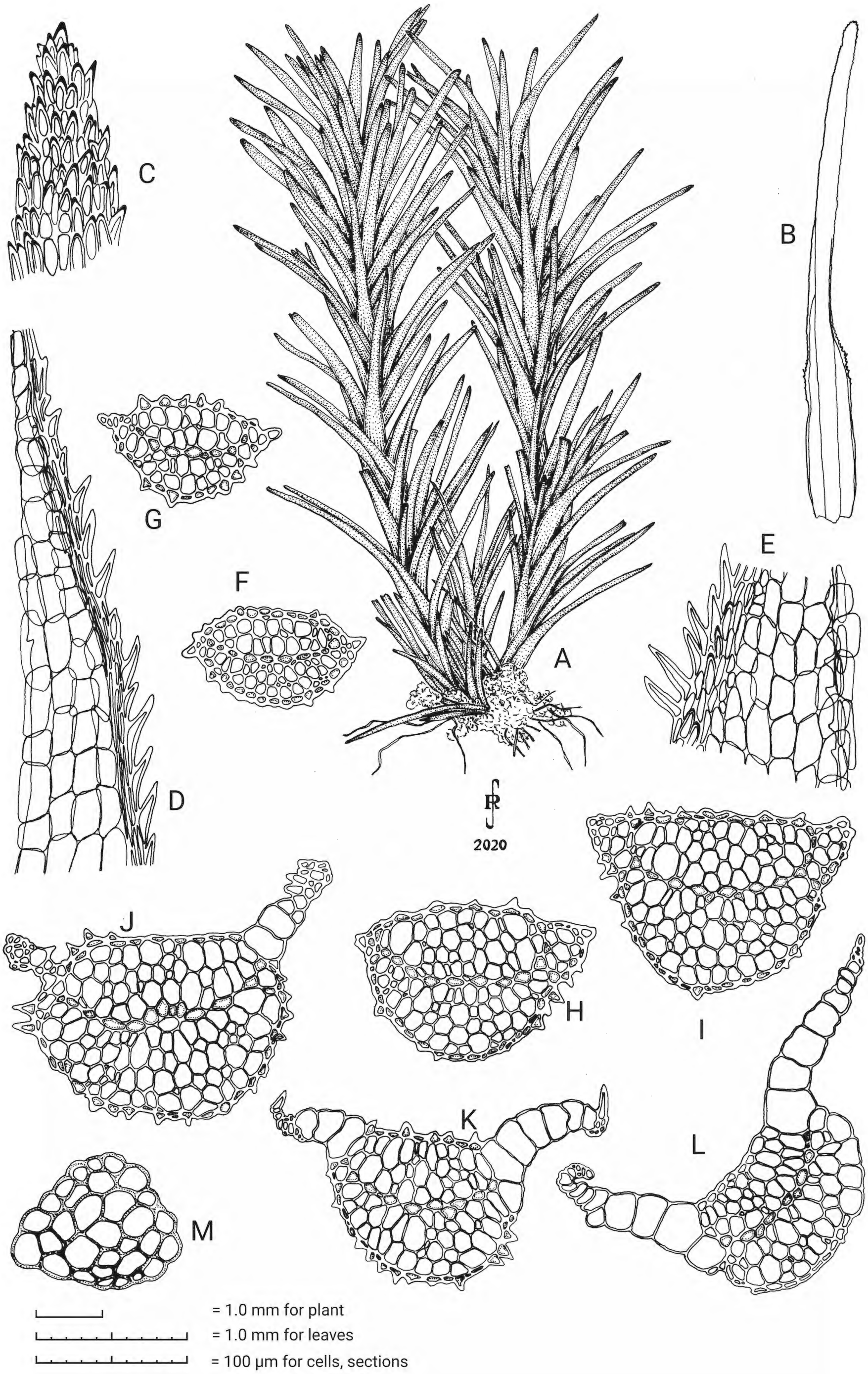

Fig. 2. *Exostratum blumei* (Nees ex Hampe) L.T.Ellis. **A:** Habit of plants, drawn moist. **B:** Stem leaf. **C:** Cells of leaf apex. **D, E:** Cells of leaf shoulder region. **F–I:** Sections of leaf limb. **J:** Section of leaf shoulder region. **K, L:** Sections of sheathing basal part of leaf. **M:** Stem section. Drawn from: *I.G.Stone 20080* (BRI).

LEUCOPHANES Brid., *Bryolog. Univ*. 1: 763 (1926).

Type: *Leucophanes octoblepharioides* Brid., *Bryol. Univ*. 1: 763 (1827), designated by R.S.Williams, Leucobryaceae in *N. Amer. Fl. Ser. 2*, 15: 159–166 (1913).

Description: Plants slender, in thick whitish to pale green tufts. Leaves erect, spreading, lanceolate to linear; lamina narrow or broad below, composed of hyalocysts with a marginal stereome of rectangular to linear cells; in upper part of leaf stereome composed of several layers of thick-walled cells. Costa widening above to occupy most of leaf width, consisting of 2 or more layers of hyalocysts enclosing a network of chlorocysts, the central part of the costa with an abaxial stereome. Gemmae occasionally present at leaf tips. Perichaetia terminal or lateral. Capsules erect, cylindrical, glossy, on long setae. Operculum long rostrate; calyptra cucullate, entire. Peristome teeth 16, linear-lanceolate, entire or occasionally split below, papillose on outer surface.

Etymology: Greek *leukos* (white) + *phaino* (appearance), referring to the very pale colour of the plants.

Distribution: A pantropical genus of ca. 40 species, of which four are represented in Australia.

Recognition: *Leucophanes* is characterised by plants whose leaves resemble those of *Leucobryum* in structure, with a layer of chlorocysts lying for the most part between 2 strata of hyalocysts, but differing markedly in having a distinct medial strand or stereome composed of stereids and guide cells. The leaves also have a marginal stereome forming a sharply differentiated border. The lamina is largely confined to the lateral wings of the sheathing base of the leaf. Capsules are erect, symmetrical, the operculum has a long beak, and the peristome consists of 16 simple teeth having the outer surface papillose. Fusiform, multicellular gemmae commonly arise from the apical region of unmodified leaves.

Key to Australian species of *Leucophanes*

1 Plants robust, to 6 cm tall; leaves broadly lanceolate, recurved or squarrose, lacking a true lamina, marginal stereome extending from apex to insertion; costa smooth abaxially ..... *L. candidum*

1: Plants small to medium-sized, <4 cm tall; leaves narrowly lanceolate to lanceolate, erect-spreading to recurved-patent, lamina present in sheathing base of leaf; costa strongly spinose or smooth on abaxial side in upper part of leaves 2

2 Leaves long and narrow, 4–9 mm long, ca. 0.4–0.5 mm wide, linear from a narrowly lanceolate sheathing base, erect-spreading to patent when moist, little altered when dry; costa strongly spinose or spiculose on abaxial surface in upper part of leaves, in section with 1 or 2 irregular layers of hyalocysts on abaxial and adaxial sides of chlorocyst layer ..... *L. angustifolium*

2. Leaves shorter, 3–6(-7) mm long, 0.3–0.4 mm wide, linear lanceolate from a slightly broader sheathing base, erect spreading, little altered wet or dry; costa with few spicules in upper part of leaves 3

3 Leaves somewhat contorted and twisted when dry; hyalocysts in surface view on abaxial surface at mid leaf oblong with sinuose walls; in section, abaxial hyalocysts bistratose in sheathing leaf base ..... *L. glaucum*

3. Leaves not contorted or twisted when dry, hyalocysts in surface view on abaxial surface at mid leaf oblong with straight walls; in section with a single layer of hyalocysts on both adaxial and abaxial sides of chlorocysts ..... *L. octoblepharioides*

3. *Leucophanes angustifolium* Renauld & Cardot, *Rev. Bot. Bull. Mens*. 9: 395 (1891).

Original material: 'Hab. Bourbon, Leg. Rev. Rodriguez'

Type: France: Réunion (Île Bourbon), Cirque de Mafate, *Rodriguez s.n.*, 1890 (holo PC0696079!d; iso S B161590!d).

Note: Type details are as annotated on the holotype packet, except that Cirque de Mafate (the current name) is called Plaine de Mafate on the packet.

Illustrations: Figure 3. Also Promma and Chantanaorrapint (2013: 26, fig. 2; 27).

Description: Plants very pale, low growing, forming loose to dense tufts; shoots to 2 cm tall. Leaves long and narrow, 4–9 mm long, ca. 0.4–0.5 mm wide, linear from a narrowly lanceolate sheathing base, erect-spreading to patent when moist, little altered when dry; apex acute to subacute; marginal stereomes well developed with 3–5 layers of stereids, margin entire or toothed, remotely serrate towards apex; medial stereome well developed, reaching to leaf apex, strongly dentate abaxially by projecting cell ends; costa carinate (channelled) to beyond mid leaf; hyalocysts of costa 2–layered almost throughout, abaxially subdivided close to the medial stereome in lower part of leaf. Sporophytes not seen in Australian material.

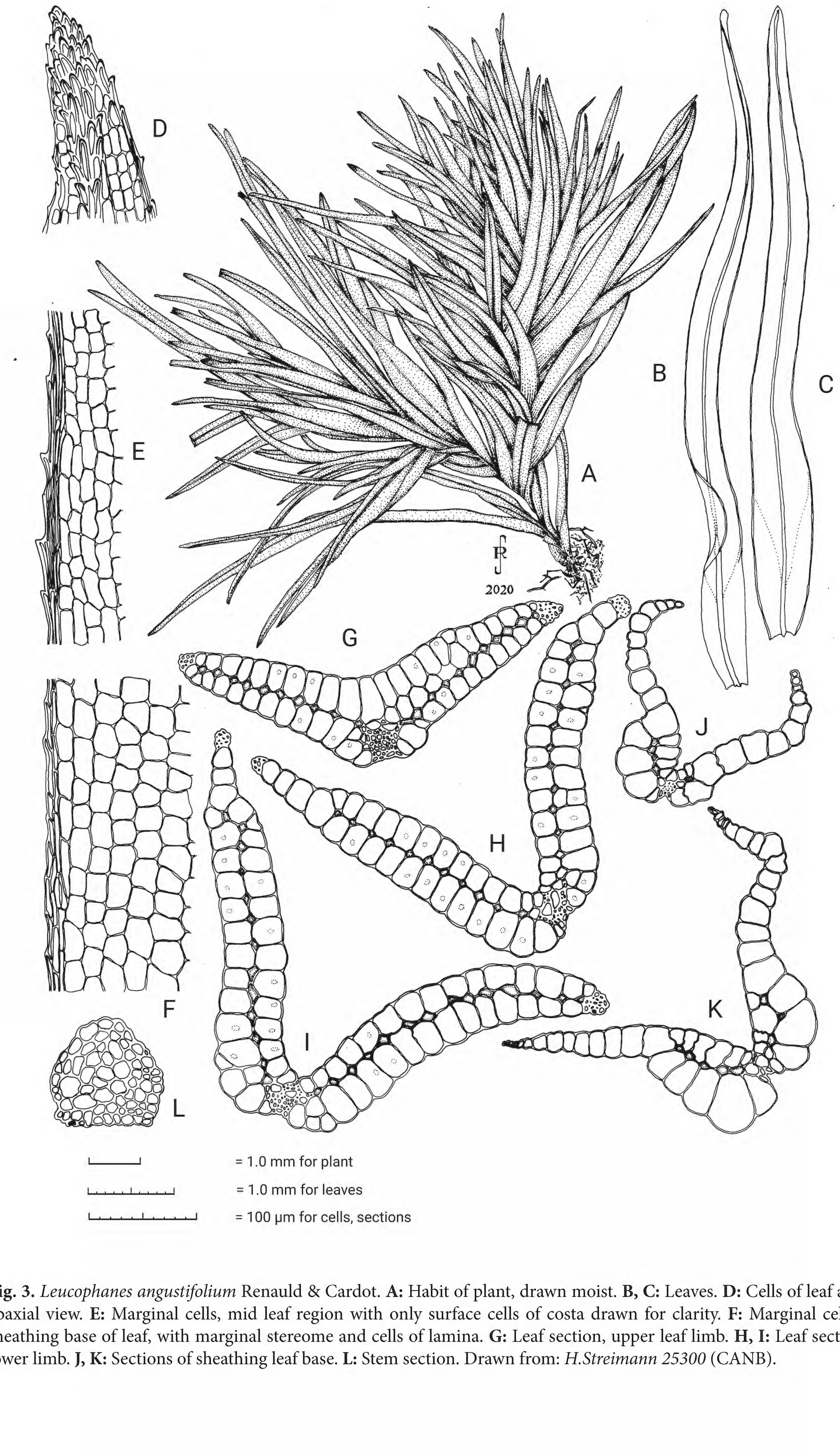

Fig. 3. *Leucophanes angustifolium* Renauld & Cardot. **A:** Habit of plant, drawn moist. **B, C:** Leaves. **D:** Cells of leaf apex, abaxial view. **E:** Marginal cells, mid leaf region with only surface cells of costa drawn for clarity. **F:** Marginal cells of sheathing base of leaf, with marginal stereome and cells of lamina. **G:** Leaf section, upper leaf limb. **H, I:** Leaf sections, lower limb. **J, K:** Sections of sheathing leaf base. **L:** Stem section. Drawn from: *H.Streimann 25300* (CANB).

Etymology: Latin *angustus* (narrow) + *folium* (leaf), referring to the shape of the leaves.

Distribution: In Australia, *L. angustifolium* is known from few collections in north-eastern Queensland (Fig. 7.3). Elsewhere pantropical, from tropical west Central Africa, Madagascar, Mauritius, Réunion, India, Sri Lanka, Japan (Ryuku Islands), Seychelles, Borneo, Malesia, the Philippines, Papua New Guinea, Pacific islands.

Habitat: *Leucophanes angustifolium* grows on tree trunks and branches, on palm trunks, and has been recorded on shaded boulders.

Recognition: Eddy (1990) describes and illustrates a very similar taxon as *L. massartii* Renauld & Cardot, a species closely related to *L. octoblepharioides*. *Leucophanes massartii* is widespread from east African islands to Malesia, New Guinea to Polynesia. Its leaves are about twice the length of those of *L. octoblepharioides* with a less extensive hyaline lamina and more extensive duplication of the abaxial hyalocysts in the leaf base. In specimens examined and attributed to *L. octoblepharioides*, the leaves are 5.0–5.5 mm long, 0.3–0.4 mm wide at the shoulders. Eddy (1990) cites leaves 4.0–8.0 mm long and 0.6–0.8 mm wide for *L. massartii*. Specimens attributed to *L. angustifolium* have leaves 4.0–7.0(–9.0) mm long, 0.5–0.7 mm wide at the shoulders. The morphological and anatomical similarity between taxa was recognised by Enroth (1990), who placed *L. massartii* (1896) in synonymy with *L. angustifolium* (1891).

Selected specimens seen: Papua New Guinea: Morobe District, Gumi–Slate Creek Divide, 25 km west of Bulolo, 1900 m alt., *H.Streimann 25300*, 19 Oct 1982, CANB: CBG 9206901.

4. *Leucophanes candidum* (Schwägr.) Lindb., *Öfvers. Förh. Kongl. Svenska Vetensk.-Akad.* 21: 602 (1865).

Basionym: *Syrrhopodon candidus* Schwägr., *Sp. musc. Frond. Suppl.* 2, 2(2): 105, t. 182, figs 1–8 (1827).

Original material: 'Legit in insula Iapama, cl. Prof. Reinwardt.'

Type: Indonesia, 'Iapama island', *C.G.Reinwardt s.n., 1815–1822* (lectotype G, *fide* Enroth 1989), not seen. Insula Saparoa [Saparua], *Anon. #H.1149, n.d.* (apparent isolecto BM000725826!d, BM000725818!d; possible isolecto K001132637!d).

Note: Reinwardt collected widely in the Dutch East Indies (now Indonesia). We do not know of any island called Iapama, or an island with a similar name, in the region. However, there is a sheet at BM with a label transcribed as 'Insula Saparoa [Saparua]' that could readily have been mis-read as 'Iapama' based on the original handwriting, and this is considered to be original material so the correct location is almost certainly Saparua Island.

Illustrations: Fig. 4. Also Eddy (1990: 43, fig. 192 a–h); Promma and Chantanaorrapint (2013: 29, fig. 4; 30, fig. 5).

Description: Plants forming compact, pale glossy whitish-green tufts or cushions. Stems slender, rigid, dark red-brown, to 6 cm long, densely leaved. Leaves typically in ± 3 rows, 3–5 mm long, 0.5–0.75(–1.0) mm wide at shoulders, erect to wide-spreading, recurved to ± squarrose from a broadened sheathing ± expanded base, arranged evenly along the stems, lanceolate to ovate-lanceolate, deeply keeled (carinate) in upper half, bordered by a narrow marginal stereome from base nearly to apex, weakly to strongly denticulate with projecting cell ends; medial stereome narrow, exposed on abaxial leaf surface, dentate in acumen and ± merged with marginal stereomes at apex; hyalocysts of costa 2-layered throughout, occasionally but never consistently subdivided on either side of medial stereome at leaf base; chlorocysts very narrow. Sporophytes frequent; seta 8–18 mm long, smooth; urn 1.2–1.5 mm long.

Etymology: Latin *candidum* (shining white), referring to the overall colour of the plants.

Distribution: *Leucophanes candidum* is known in Australia from Mossman Gorge, north-eastern Queensland (Fig. 7.4). Elsewhere *L. candidum* is known from Central Africa, from western Indian Ocean islands to Sri Lanka, south east Asia, China, Malesia to Samoa.

Habitat: *Leucophanes candidum* grows as an epiphyte on bark in moist shaded lowland rainforest, mainly below 400 m. When growing in more exposed sites, the plants may be more compact and develop a brownish pigmentation.

Recognition: Some plants of *L. candidum* may be difficult to distinguish from *L. glaucum*, a variable taxon with a significant synonymy attesting to its variability. Loosely clumped plants may develop the ± tristichous leaf arrangement but more compact forms tend to lose this. Exposure and humidity levels seem to have a considerable influence on growth habit (Eddy 1990). Compact forms of *L. candidum* differ from *L. leucobryoides* in having deeply keeled rather than a ± flattened upper leaf blade. Compact forms of *L. glaucum* differ from compact forms of *L. candidum* in having duplicated layers of hyalocysts adjacent to the medial stereome in the basal part of the leaf.

Selected specimens seen: Queensland: Cook District; Mossman Gorge, *W.B.Schofield 90054, I.G.Stone and M.I.Schofield*, 05 Sept 1987, UNSW B117889.

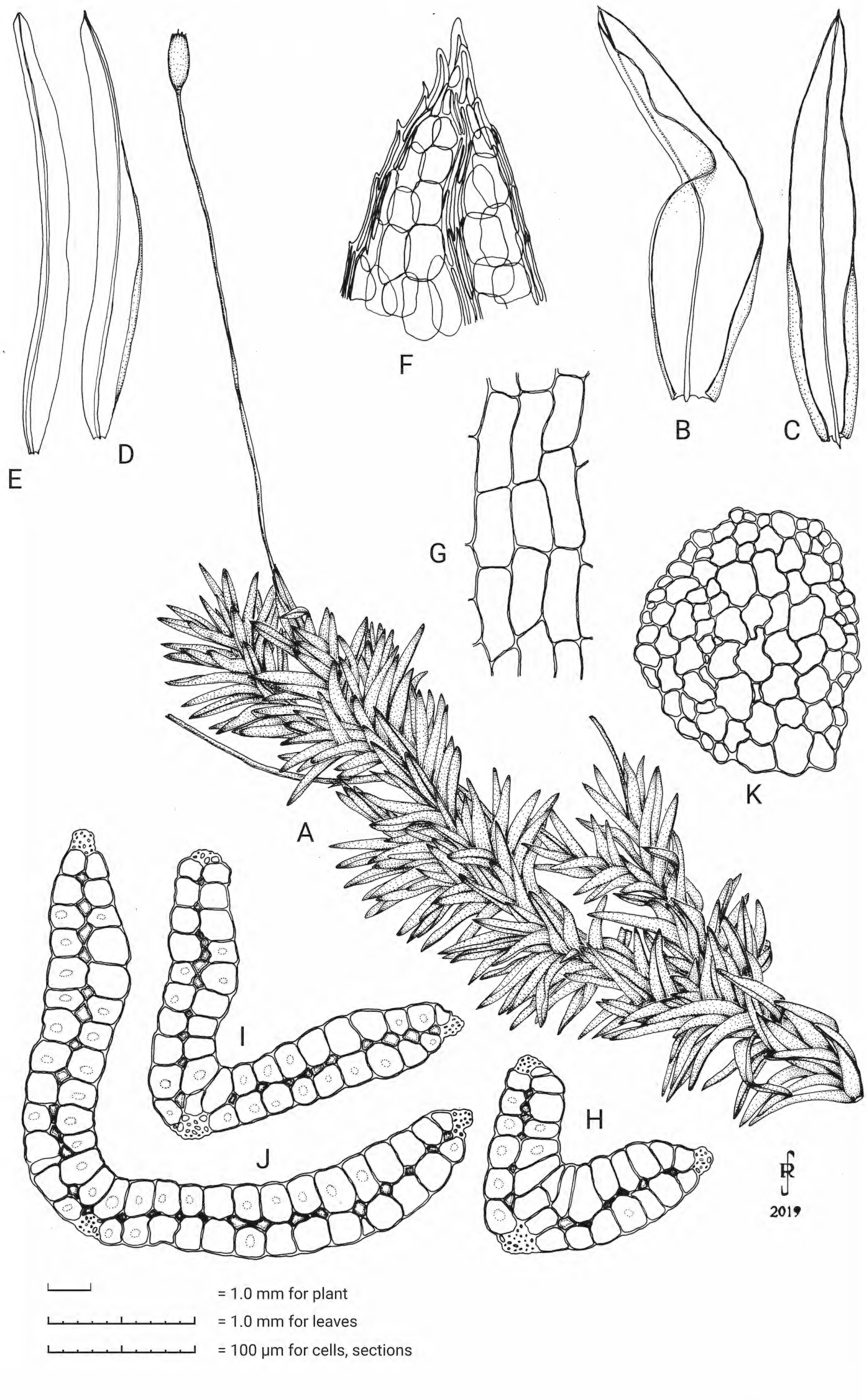

Fig. 4. *Leucophanes candidum* (Schwägr.) Lindb. **A:** Habit of plant, drawn moist. **B, C:** Stem leaves. **D, E:** Inner perichaetial leaves. **F:** Cells of leaf apex. **G:** Exothecial cells from mid capsule. **H–J:** Sections of leaves. **K:** Stem section. Drawn from: *W.B.Schofield et al. 90054* (UNSW).

5. *Leucophanes glaucum* (Schwägr.) Mitt., *J. Proc. Linn. Soc. Bot. Suppl.* 1: 25 (1859).

Basionym: *Syrrhopodon glaucus* Schwägr., *Sp. Musc. Frond. Suppl.* 2(2): 103, pl. 181 (1827).

Original material: 'Legit in insula Rauwack Moluccarum et cum Octoblepharo albido in insulis Marianas c. Gaudichaud.'

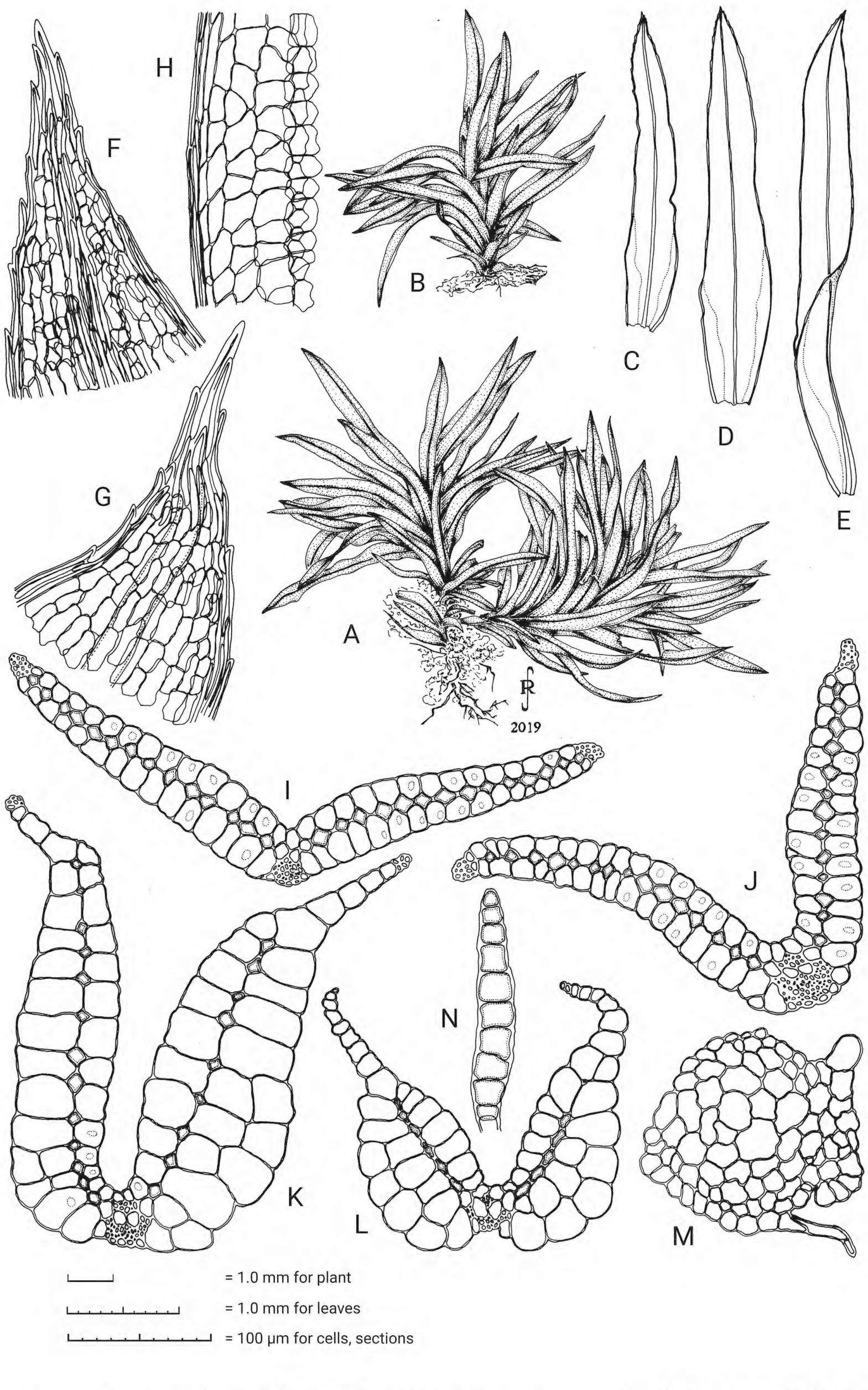

Fig. 5. *Leucophanes glaucum* (Schwägr.) Mitt. **A, B:** Habit of plants, drawn moist. **C–E:** Leaves. **F, G:** Cells of leaf apex (F – abaxial,G – adaxial). **H:** Cells from upper part of leaf base, showing marginal stereome, lamina, and edge of costa. **I, J:** Sections of leaves at mid lamina. **K, L:** Sections of leaf sheathing base, showing 2–3 layered abaxial hyalocysts. **M:** Stem section. **N:** Gemma. Drawn from: *D.A.Meagher and A.Cairns WT-167, BRI.*

Type: Mariana Islands, leg. *Gaudichaud s.n.*, *n.d.*, (pre 1827) (lectotype G, *fide* Enroth 1989), not seen. Syntypes in protologue: Indonesia, Maluku Islands, Rauwack Island, *sine leg.*, *s.n.*, *s.d.* (pre 1827), PC-0696056!d, PC-0696054!d.

Presumably also Rawak, *C.Gaudichaud #25*, 1809 (PC0696053!d, PC0696055!d); Isle de Rawack [Rauwack], *C.Gaudichaud #10=9/25* (BM 000726071!d, BM 000726072!d, BM 000726073!d, BM 000726074!d).

Illustrations: Fig. 5. Eddy (1990: 44, fig. 193a–h; 46, fig. 194a–e; 47, fig. 195a–d); Promma and Chantanaorrapint (2013: 32, fig. 6; 33, fig. 7).

Description: Plants forming small to medium-sized, pale greyish-green to whitish- or yellowish-green tufts; stems 1–3 cm tall, thin, reddish-brown, lacking a central strand, simple or branched. Leaves erect-spreading, narrowly lanceolate to linear-lanceolate, tapering upwards to a broadly or narrowly acute apex from an erect sheathing base; 3–6(–7) mm long, 0.3–0.4(–1.0) mm wide at shoulders; channelled to apex or nearly so; marginal stereomes well-developed, up to 3 cells deep, 3–5 cells wide, margins ± dentate above, rarely entire; medial stereome well developed, exposed abaxially, ± dentate in upper limb, percurrent to excurrent and joining with marginal stereomes at apex; hyalocysts of costa 2-layered above, thickened to 2–3 layers for some distance above insertion on abaxial side of chlorocyst layer of costa on either side of medial stereome; chlorocysts relatively large in section, forming an almost continuous stratum in upper limb. Hyaline lamina confined to lower half of leaf, of variable width, 4–8 cells either side of central strand.

Etymology: Latin *glaucum* (the colour of the sea, bluish green), referring to the overall colour of the plants.

Distribution: Known in Australia from northern Northern Territory and north-eastern Queensland (Fig. 7.5). Widespread throughout Malesia to Papua New Guinea, Polynesia and New Caledonia. Also known from the Seychelles, India, Sri Lanka, south east Asia to China, Japan and the Philippines.

Habitat: *Leucophanes glaucum* grows on the bark of trees and on rotting logs in lowland forests, especially in coastal areas, seldom above 400 m altitude.

Recognition: In the field, the bleached colour in combination with the distinct medial stereome is typical of the genus. The narrow non-squarrose leaves should provide separation from the usually much taller *L. candidum*, where the leaf arrangement is ± tristichous. *Leucophanes octoblepharioides* has a ± flattened upper limb not deeply keeled as in *L. glaucum*. Eddy (1990) noted that *L. glaucum* was a very variable taxon with a number of synonyms and concluded that the "key" characters that had been used to differentiate these morphologically related taxa intergraded across arrange of forms, concluding that *L. glaucum* was a single, highly polymorphic taxon. Further study, particularly including molecular analyses, is needed to satisfactorily resolve the issue.

Selected specimens seen: Queensland: Cook District: Tchupala Falls, *D.A.Meagher and A.Cairns WT-013*, 14 Sept 2012, BRI AQ1016554; Cape Tribulation National Park, Dubuji Boardwalk, Myall Creek, *D.A.Meagher and A.Cairns WT-167*, 12 May 2013, BRI AQ1016922.

6. *Leucophanes octoblepharioides* Brid., *Bryol. Univ.* 1: 763 (1827).

Original material: 'In insula Java unde clariss. Nees v. Esenbeck habuit et humanissime in usum communicavit, et in regione Nepal Indiae ex Herbario Candolleano caespitose ad terram habitat.'

Type: Syntypes in protologue: Indonesia, Java, *s.coll. s.n.*, *s.d.* (pre-1827) (syn E 00011684, *fide* L. Ellis in annot.); Nepal, *s.leg.*, *s.n.*, *s.d.* (pre-1827) (syn *n.v.*). Possibly also: Java, *s.c.*, *s.n.*, *n.d.* (PC0696027!d, PC0696028!d, PC0696029!d).

Note: The isosyntype is annotated as having been collected by Nees von Esenbeck in 1830, but neither Christian nor (Theodor) Friedrich ever travelled outside Europe. We have found no trace of the other syntype. The annotation probably only indicates that Nees von Esenbeck sent the specimen to Greville in that year.

Illustrations: Figure 6. Also: Eddy (1990: 47, fig. 196a–g); Promma and Chantanaorrapint (2013: 34, fig. 8; 35, fig. 9).

Description: Plants whitish, pale green, forming low tufts. Stems short, reddish-brown. Leaves erect-spreading when moist, little altered when dry, linear-lanceolate, from a slightly wider sheathing base tapering gradually to a subacute or acute apex, 3–7 mm long, 0.3–0.4 mm wide at shoulders, 0.15–0.20 mm wide in limb; nearly plane or slightly channelled in upper limb, channelled in lower half of limb; leaf apex broadly acute, dentate; marginal stereomes reaching apex, entire to dentate, at least near apex; medial stereome well-developed, exposed abaxially, reaching to apex; costa bistratose almost throughout, abaxial hyalocysts becoming subdivided near medial stereome only in extreme base of leaf; chlorocyst layer situated closer to abaxial side of leaf in mid to upper limb.

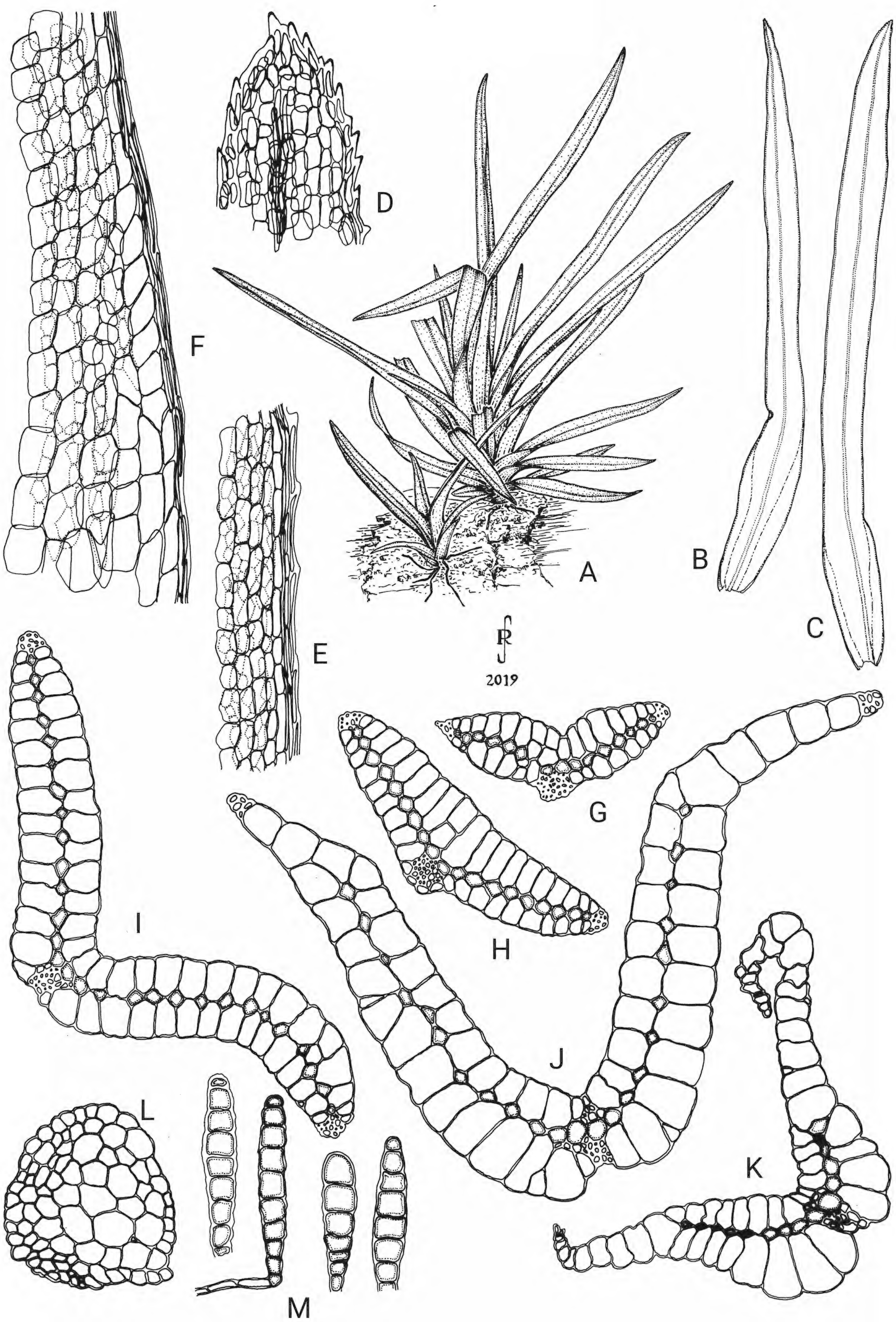

Fig. 6. *Leucophanes octoblepharioides* Brid. **A:** Habit of plant, drawn moist. **B, C:** Leaves. **D:** Cells of leaf apex, abaxial view. **E:** Marginal cells from mid limb. **F:** Cells of leaf shoulder region, with cells of costa, lamina and marginal stereome. **G–I:** Sections of leaf limb. **J:** Section of leaf shoulder region. **K:** Section of leaf base near to the insertion. **L:** Stem section. **M:** Gemmae. Drawn from: *A.J.Franks AJF1407005B* (BRI).

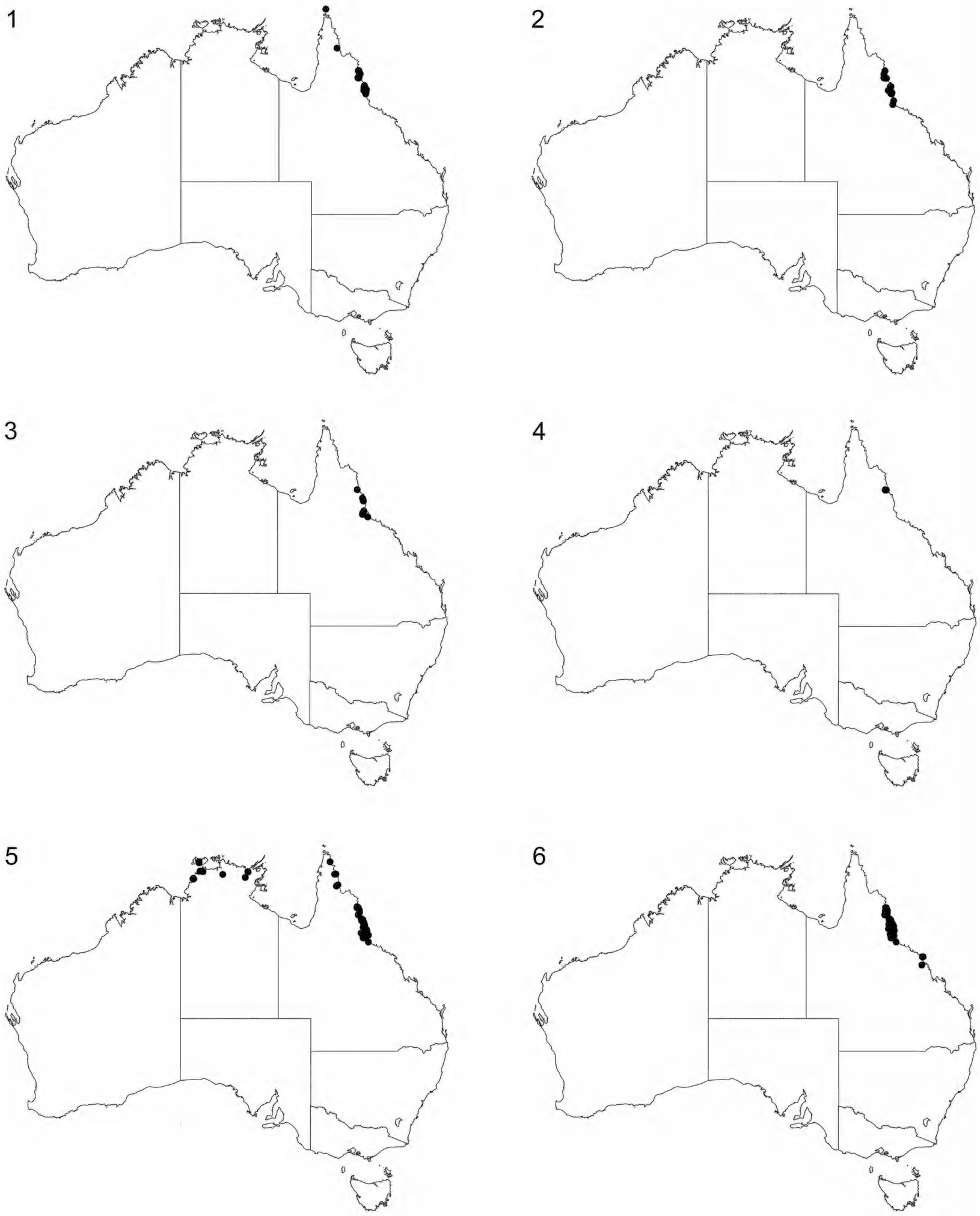

Fig. 7. Known distributions of *Arthrocormus*, *Exostratum* and *Leucophanes* species in Australia. **1** *Arthrocormus schimperi*. **2** *Exostratum blumei*. **3** *Leucophanes angustifolium*. **4** *Leucophanes candidum*. **5** *Leucophanes glaucum*. **6** *Leucophanes octoblepharioides*. Source: Australia's Virtual Herbarium (accessed 8 June 2021).

Etymology: *Octoblepharum* + *–oides* (resembling), referring to the similarity in appearance to that genus.

Distribution: Known in Australia from north-eastern Queensland from Daintree to Finch Hatton Gorge (Fig. 7.6). Elsewhere, widespread throughout the Indo-Pacific region, from tropical central Africa, Mauritius, Seychelles to India, Nepal, Sri Lanka, south east Asia to China (Hainan Island), Japan (southern islands), Guam, Malesia, the Philippines, to Polynesia and New Caledonia.

Habitat: Epiphytic on bark of trees, particularly on fibrous bark, tree ferns, tree roots.

Recognition: *Leucophanes octoblepharioides* resembles *L. glaucum* but is typically shorter stemmed and with larger leaves (Eddy 1990). However, in Australian collections there seems to be little difference in leaf dimensions. The more or less flattened (rather than deeply channelled) leaves should serve to differentiate *L. octoblepharioides* from *L. glaucum*. In doubtful cases, leaf sections in the lower part of the leaf, close to the insertion, should show that in *L. octoblepharioides* there is little subdivision of the bistratose abaxial hyalocysts.

The species is somewhat similar in appearance to *Octoblepharum albidum*, but in that species the leaves lack a medial stereome.

In *Leucophanes angustifolium* the adaxial surface of the leaf may be channelled for a greater distance above the sheathing base, and there is less duplication of the abaxial hyalocysts near the leaf insertion. Eddy (1990) indicated that leaf length and plant size, at least for mature plants, may also be a means of separating this species. However, in Australian specimens, this may not be definitive. With such morphological similarity between *L. angustifolium* and *L. octoblepharioides*, there may be little reason to maintain their separation and, if united, *L. octoblepharioides* (1827) would take nomenclatural precedence over *L. angustifolium* (1891).

Selected specimens seen: Queensland: North Kennedy District; Conway National Park, Kingfisher Circuit, 158 m a.s.l., *A.J.Franks AJF1407005B*, 01 July 2014, BRI AQ0913185; Cook district, Wooroonooran National Park, K-tree Track, 9.3 km from turn off from Palmerston Highway, *D.A.Meagher and A.Cairns WT-642*, 29 May 2015, BRI AQ1019817.

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References

Cairns A, Meagher D, Seppelt RD, Franks AJ (2020) The moss family Octoblepharaceae A.Eddy ex M.Menzel in Australia. *Telopea* 23: 237–244. http://dx.doi.org/10.7751/telopea14820

Catcheside DG (2012a) Australian Mosses Online. 13. Calymperaceae: *Arthrocormus*. http://www.anbg.gov.au/abrs/Mosses_online/12_Calymperaceae/Calymperaceae_Arthrocormus.pdf (accessed 24 November 2020)

Catcheside DG (2012b) Australian Mosses Online. 13. Calymperaceae: *Exostratum*. http://www.anbg.gov.au/abrs/Mosses_online/12_Calymperaceae/Calymperaceae_Exostratum.pdf (accessed 24 November 2020)

Catcheside DG (2012c) Australian Mosses Online. 13. Calymperaceae: *Leucophanes*. http://www.anbg.gov.au/abrs/Mosses_online/12_Calymperaceae/Calymperaceae_Leucophanes.pdf (accessed 24 November 2020)

Dozy F, Molkenboer JB (1846) *Musci frondosi inediti archipelagi Indici sive descriptio et adumbration muscorum frondosorum in Insulis Java, Borneo, Sumatra, Celebes, Amboina nec non in Japonia nuper detectorum minusve cognitorum*. Fascicle II. H.W. Hazenberg & Soc.: Lugduni Batavia. https://www.biodiversitylibrary.org/item/124609#page/105/mode/1up

Eddy A (1990) *A handbook of Malesian mosses. Vol. 2. Leucobryaceae to Buxbaumiaceae*. Natural History Museum Publications, London.

Ellis LT (1985) A taxonomic revision of *Exodictyon* Card. (Musci: Calymperaceae). *Lindbergia* 11(1): 9–37. https://www.jstor.org/stable/20149539

Enroth J (1990) Bryophyte Flora of the Huon Peninsula, Papua New Guinea, XXXVI, Leucobryaceae (Musci). *Acta Botanica Fennica* 139: 65–120.

Promma C, Chantanaorrapint S (2013) The genus *Leucophanes* (Calymperaceae, Bryophyta) in Thailand. *Thai Forest Bulletin (Botany)* 41: 23–38. https://li01.tci-thaijo.org/index.php/ThaiForestBulletin/article/view/24096

Stafleu FA, Cowan RS (1979) *Taxonomic literature*. Volume II: H–Le. Second edition. Bohn, Scheltma & Holkema (Utrecht) & dr. W. Junk b.v. (The Hague). https://doi.org/10.5962/bhl.title.48631

Touw A (2013) *Original specimens kept in the herbarium of Naturalis Biodiversity Center (section Nationaal Herbarium Nederland) of Asian and South American moss taxa published by F. Dozy, J.H. Molkenboer, R.B. van den Bosch and C.M. van der Sande Lacoste*. Naturalis Biodiversity Center, section NHN – Electronic Publication, updated 16 August 2013. https://repository.naturalis.nl/pub/472590

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Nymphaea kakaduensis (Nymphaeaceae), a new species from the northern portion of the Northern Territory, Australia

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Abstract

Nymphaea kakaduensis C.B.Hellq., A.Leu & M.L.Moody (Nymphaeaceae) is described from Kakadu National Park, Northern Territory. This new species is endemic to the "Top End" of the Northern Territory and was formerly included in *N. violacea* Lehm. The distinct floral form *of N. kakaduensis* of having generally smaller flowers with blunt-tipped petals and different coloration than *N. violacea* instigated a genetic study of taxa from the region. The cpDNA *trn*L (UAA) - *trn*F (GAA) intergenic spacer region was sequenced from samples from across northern Australia and a haplotype network analysis was conducted. Plants from populations that had the distinct floral form of *N. kakaduensis* are found to be genetically distinct from *N. violacea* in northern Australia sharing 4 SNPs and a notable 23 bp indel in the cpDNA intergenic spacer region to support the morphological attributes and species designation.

Introduction

The number of *Nymphaea* L. species recognised in Australia has expanded considerably since Conard's (1905) treatment of the genus determined all *Nymphaea* in Australia to be *N. gigantea* Hook., with *N. violacea* Lehm. designated as a variety. Extensive collections and studies by numerous investigators over the last century have now revealed a diversity of Australian *Nymphaea* species (*e.g.* Aston 1970; Conard 1905; Borsch *et al.* 2007; Jacobs 1992, 1994; Cowie *et al.* 2000; Jacobs and Hellquist 2006, 2011; Jacobs and Porter 2007; and Löhne *et al.* 2008). Today, there are 18 native species of Australian *Nymphaea* described (Jacobs and Hellquist 2011).

Conard's (1905) treatment of *Nymphaea* considered *N. gigantea* var. *violacea* (Lehm) Conard as a smaller form within *N. gigantea* and Aston (1970) reiterated this interpretation. *Nymphaea violacea* was again formally recognised with lectotypes designated by Jacobs (1992) and it is now accepted as a distinct species (Short 2000; Jacobs and Porter 2007). *Nymphaea violacea* is abundant throughout the Australian tropical regions of Queensland, Northern Territory and Western Australia and it occurs in New Guinea (Jacobs and Porter 2007). It is highly variable with flowers that may be blue, mauve, pink or white. The petals have been described as acute-tipped, blunt or intermediate between the two characteristics. The sepals and petals are frequently ascendant giving the flower an acute floral profile (Fig. 1A).

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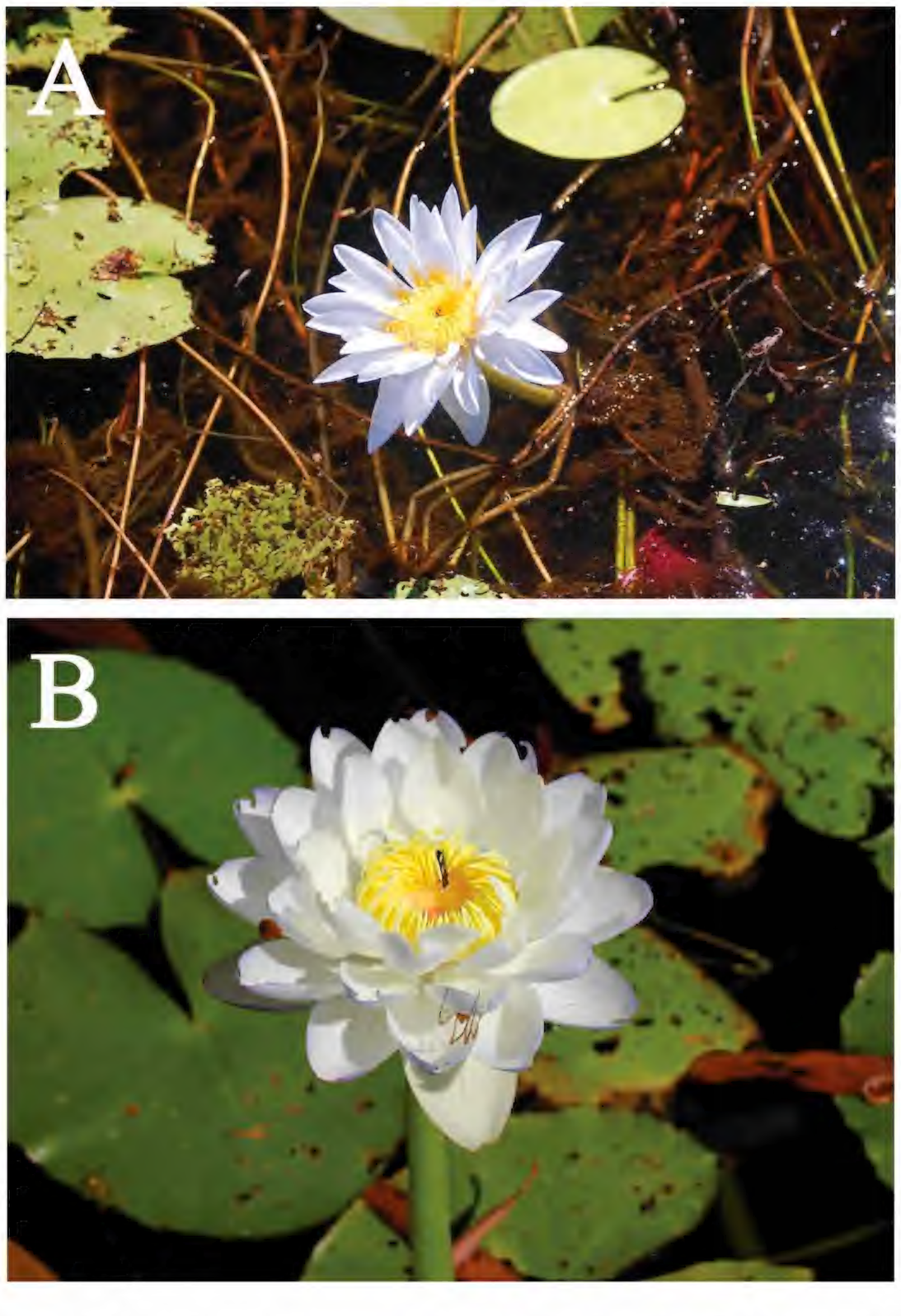

Fig. 1. Floral characteristics of *Nymphaea violacea* and the closely related *N. kakaduensis*. A. *N. violacea* with characteristic acute oblanceolate petals with tinges of bluish coloration (Kakadu population), B. *N. kakaduensis* with white coloured, blunt ovate–elliptic petals tinged with pale blue at the apex and along the margins (Lake Jabiru population). Photos: C.B. Hellquist.

Kakadu National Park is located in the "Top End" or northernmost region of the Northern Territory, east of Darwin and west of the Arnhem Land Aboriginal Reserve. The region has many wetlands, rivers, streams and billabongs that are well known for their waterlily populations. The senior author first visited Kakadu in 1997, with subsequent collecting trips to the area in 2002, 2005, and 2011. One of the largest wetland complexes within Kakadu National Park is the floodplain billabong of the South Alligator River at Yellow Waters (Cowie *et al.* 2000). *Nymphaea* taxa found in this region include the night blooming species *N. pubescens* Willd. and the day-blooming *N. macrosperma*, Merr. & L.M. Perry, *N. hastifolia* Domin., *N. nouchali* Burm. f. and *N. violacea* (see key below). Morphologically distinctive hybrid *N. violacea* × *N. macrosperma* have also been identified in the region and have been confirmed using molecular data (Löhne *et al.* 2008).

Nymphaea violacea is the most widespread and abundant species in Kakadu National Park and is common in Yellow Waters with many of the open water plants having characteristic large, blue flowers with acute petals (Fig. 1A). In Jim Jim Creek, its billabong system and surrounding wetlands, we found multiple sites inhabited by populations initially believed to be *N. violacea* but which, upon closer observation, appeared to be morphologically distinct (Fig. 2A). Initially, the darker green upper leaf surface drew our attention to plants now described as *N. kakaduensis*, as they were mixed among the lighter green leaves of *N. violacea* (Fig. 2B). The plants had flower buds that were blunt and wider (Fig. 2C) compared to the typically shorter angular buds of *N. violacea*. In addition, the flowers of *N. kakaduensis* were smaller with blunt-tipped petals and often a slight pink hue (Fig. 2D-E), but could be infused with more blue coloration (Fig. 2B) like those found in Jim Jim Billabong and Lake Jabiru. The fruiting peduncles were also coiled at the type locality (Fig. 2E); however, more field observations will be required to determine if this characteristic is consistent across populations. Here, we describe and provide genetic support for plants with this form as a new species of *Nymphaea* from the Northern Territory designated as *N. kakaduensis*.

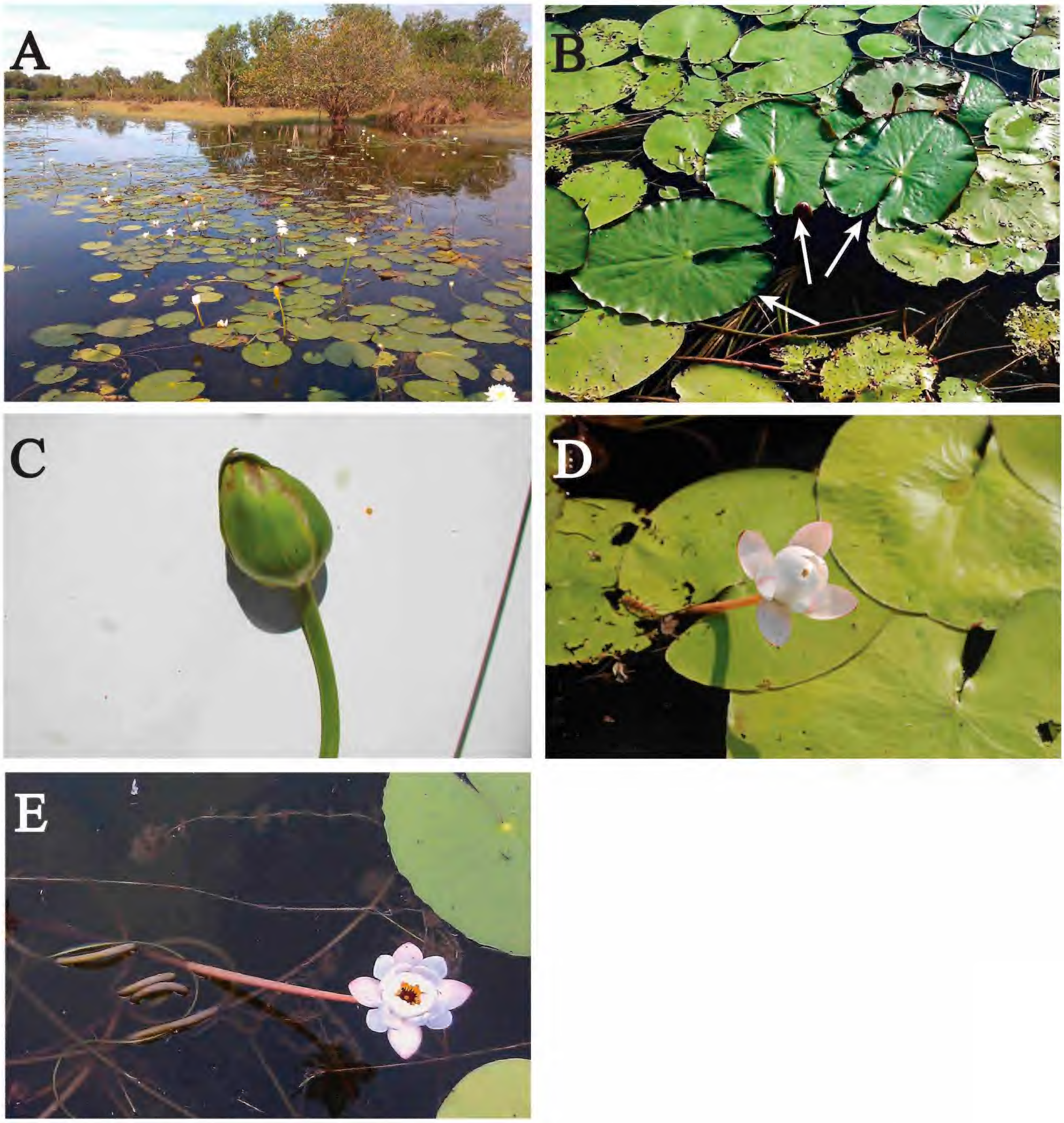

Fig. 2. Habitat and characteristics of *Nymphaea kakaduensis*. A. Plants of the type location, Jim Jim Creek, Kakadu National Park. B. Dark green leaves of *N. kakaduensis* (see arrows) surrounded by leaves of *N. violacea*. C. Blunt flower bud. D. White flower infused with pink. E. Coiled peduncles. Photos: C.B. Hellquist and A. Leu.

Methods

DNA was extracted from dried leaf material of 25 samples of *Nymphaea* from 24 populations in northern Australia (Table 1). Five samples are recognised as having morphological features of *N. kakaduensis* and 14 of *N. violacea*. *Nymphaea macrosperma* (6 accessions) was also included to address if there was evidence that *N. kakaduensis* was a result of recent hybridisation between *N. macrosperma* and *N. violacea* as these species are known to hybridise in the region. DNA extractions were performed using the DNeasy Plant Mini Kit (Qiagen), following the manufacturer's protocol. The polymerase chain reaction (PCR) was used to amplify the cpDNA *trn*L (UAA) – *trn*F (GAA) intragenic spacer region using the primers TabF and TabC (Taberlet *et al.* 1991) following the protocol of Shaw *et al.* (2005). The PCR products were treated with ExoSAP-IT (Affymetrix) to eliminate unincorporated primers and dNTPs before sequencing. The PCR products were sequenced using the same primers used for PCR and BigDye terminator chemistry (Applied Biosystems), on an ABI 3130xl automated sequencer (Applied Biosystems) at the UTEP Genomics Analysis Core in the Border Biomedical Research Center.

Table 1. Specimens used for network analysis. Included are the herbarium voucher, coordinates, location description and GenBank accession numbers.

Taxon	Voucher	Location & Coordinates	GenBank #
N. kakaduensis	Jacobs & Hellq. 8792, DNA	Lake Jabiru, Jabiru, Kakadu N.P., N.T. 12°40.429'S, 137°09.546'E	MW427905
N. kakaduensis	Jacobs & Hellq. 8799, B, BRIT, PERTH	Jim Billabong, Kakadu N.P., N.T. 12°56.538'S, 132°33.076'E	MW427903
N. kakaduensis	Hellq., Leu, F. Baird & D. Miller 17198, CNS, DNA, GH, NSW	Billabong, Yellow Waters, Kakadu N.P., N.T., 12°54.523'S, 132°31.629'E	MW427904
N. kakaduensis	Hellq., Leu & F. Baird 17211, CNS, BRIT, DNA, GH, NSW	Billabong, upper end of Jim Billabong Creek, Kakadu, N.P., N.T., 12°57.676'S, 132°34.516'E	MW427902
N. kakaduensis	Hellq., Leu & F. Baird 17212, BRI, DNA, NSW	Billabong, upper end of Jim Billabong Creek, Kakadu, N.P., N.T., 12°57.676'S, 132°34.516'E	MW427901
N. macrosperma	Jacobs & Hellq. 8796, B, DNA, GH, K, NSW	Four Mile Hole, Wildman River, Kakadu N.P., N.T., 12°54'S, 132°31'E	MZ069075
N. macrosperma	Jacobs & Hellq. 8802, CNS, DNA	Top Swamo, Yellow Waters, Kakadu N.P., N.T., 12°54'S, 132°31'E	MZ069076
N. macrosperma	K. Wilson 10143, Jacobs & Hellq.	Parry's Lagoon N.R., SE.of Wyndham, W.A., 15°32.969S, 128°15.592	MZ069077
N. macrosperma	Hellq., Wiersema & Lahriing 16181, DNA, NSW	Island Billabong, Kakadu N.P., N.T., 12°33'31"S, 132°52'30"	MZ069078
N. macrosperma	Hellq. & Leu 17187, CNS, DNA	Elsey River crossing of Roper R., N.T., 15°00'42"S, 133°14'22"E	MZ069074
N. macrosperma	Hellq, 17206, Leu, F. Baird & D. Miller, CNS, DNA	Yellow Waters, Kakadu N.P., N.T., 12°53'59"S, 132°30'45"E	MZ069073
N. violacea	Jacobs & Hellq. 8779, B, CNS, DNA, NSW	Kangaroo Creek, Borroloola Rd., N.T., 16°49.841'S, 137°09.546'E	MW427899
N. violacea	Jacobs & Hellq. 8806, NSW	Fogg Dam, Middle Point, N.T., 12°33.631'S, 131°17.989'E	MW427898
N. violacea	Jacobs & Hellq. 8860, B, DNA, NSW, PERTH	Hidden Valley, Kununurra, W.A., 15°46.334'S, 128°45.051'E	MW427895
N. violacea	Jacobs & Hellq. 8863, B, DNA, GH, NSW	Little Roper River, Mataranka, N.T., 15°46.334'S, 128°45.051'E	MW427900
N. violacea	Hellq. & Leu 16589, CNS	Lagoon N. of Mt. Molloy cemetery, Qld., 16°41.12.4'S, 145°19.34'E	MW427892
N. violacea	Hellq. & Leu 16755, GH	Stockpond 8 km S. of Coen, Qld., 14°00.288'S, 143°11.436'E	MW427894
N. violacea	Hellq. & Leu 16754, DNA	Palmer River Roadhouse lagoon, Qld., 16°06.443'S, 144°46.630'E	MW427893
N. violacea	Hellq. & Leu 16759, CNS	Langi Lagoon, Mungkan Kaanju N.P., Qld., 13°27.052'S, 142°42.49'E	MW427897
N. violacea	Hellq. & Leu 17185, CNS, DNA	Mataranka, swamp, N.T., 14°55.091'S, 138°04.041'E	MW427886
N. violacea	Hellq., Leu, F. Baird & D. Miller, 17200, CNS, DNA	Flooded roadside, Cooinda, Kakadu N.P., N.T., 12°53.817'S, 132°31.125'E	MW427889
N. violacea	Hellq., Leu, F. Baird & D. Miller 17207, CNS, DNA	Yellow Waters, Kakadu N.P., N.T., 12°53.988'S, 132°30.758'E	MW427888
N. violacea	Hellq., Leu, F. Baird & D. Miller 17209, CNS, DNA, NSW	Yellow Waters, Kakadu N.P., N.T., 12°53.707'S', 132°30.317'E'	MW427891
N. violacea	Hellq. & Leu 17217, BRI	Toomba Station,south of Lolworth Creek, Qld., 19°59.297'S, 145°33.858'E	MW427887
N. violacea	Hellq. & Leu 17220, CNS	Toomba Station; flooded grassland, Qld., 18°58.898'S, 145°35.197'E	MW427890

Sequence chromatograms were assembled and edited in Sequencher 4.2 (GeneCodes Corp.). The *trn*L (UAA) – *trn*F (GAA) region was then manually aligned using MacClade 4.08 (Madison and Madison 2000) and indels were determined following Moody and Les (2010). The indels were expressed as binary characters (T/A) at the end of the sequence following Moody *et al.* (2016) to be used for haplotype network analyses. Haplotype networks were constructed from the cpDNA region sequences using statistical parsimony as implemented in TCS 1.21 (Clement *et al.* 2000), with a 95% connection limit and with gaps treated as missing data.

Molecular Results

The final cpDNA *trn*L (UAA) – *trn*F (GAA) region alignment for the haplotype network included 25 accessions and had a length of 902 base pairs. There were 8 haplotypes identified as a result of the network analysis (Fig. 3). All *N. kakaduensis* accessions were found to belong to three haplotypes that varied by 1 or 2 single nucleotide polymorphisms (SNPs) and were divergent from all *N. violacea* accessions by at least 4 SNPs and 2 indels (23 bp and 2 bp). *Nymphaea kakaduensis* accessions were divergent from *N. macrosperma* accessions by 5 SNPs and 3 indels (27 bp, 9 bp and 7 bp). Most *N. violacea* sampled shared a common haplotype, but there was some variation based on SNPs.

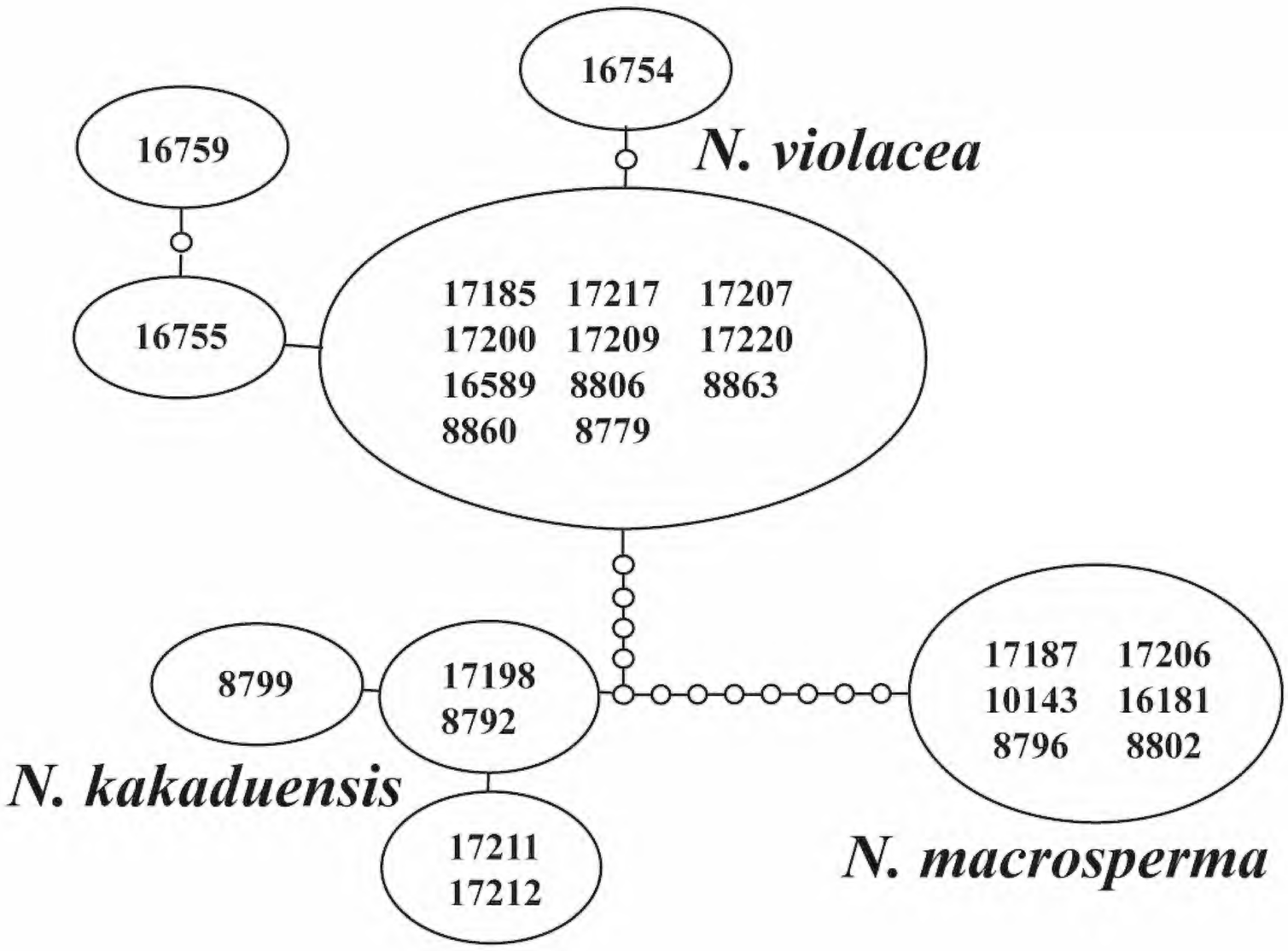

Fig. 3. Haplotype network based on cpDNA *trn*L (UAA) – *trn*F (GAA) using statistical parsimony for *Nymphaea kakaduensis*, *N. macrosperma* and *N. violacea* accessions from Northern Australia. Ovals represent haplotypes, and size is proportional to number of accessions sharing a given haplotype. Lines between small circles indicate mutational steps between haplotypes (SNPs or Indels). Each number represents accessions presented in Table 1.

Discussion

Floral characteristics were consistent among sampled population of *N. kakaduensis*. Flowers of *N. kakaduensis* had most petals with a blunt apex and ovate to elliptic shape; whereas, *N. violacea* has oblanceolate petals with a commonly acute apex. Sepals are also generally shorter in *N. kakaduensis* (up to 6 cm) compared to *N. violacea* (up to 11.5 cm). Seed size has been useful to distinguish Australian *Nymphaea* (Jacobs and Porter 2007; Jacobs and Hellquist 2011). There was consistent differences in seed size between *N. kakaduensis* (on average 2.0 × 1.3 mm from five populations) and *N. violacea* (on average 1.5 × 0.9 mm from 17 "Top End" populations). Seed size measured from 25 Queensland populations of *N. violacea* were similar to those from the "Top End" of the Northern Territory at an average of 1.5 × 1.0 mm. The seeds of *N. kakaduensis* also have a latitudinal ridge that is lacking in *N. violacea*.

Given the floral variation and seed differences between *N. kakaduensis* and *N. violacea,* molecular data provides further evidence for the new species designation. The cpDNA haplotype network indicated that samples with the aforementioned morphological variation from four populations in the Kakadu region were genetically distinct from *N. violacea* and *N. macrosperma* (Fig. 3), which are commonly found in the same waterbodies as *N. kakaduensis*. The *trn*L (UAA) – *trn*F (GAA) intragenic spacer has been considered a useful species level DNA barcode (Hollingsworth *et al.* 2011) and has been used for this purpose in other groups for species identification (e.g. Bączkiewicz *et al.* 2017; Liu *et al.* 2012). In this case, the molecular data support the morphological evidence for *N. kakaduensis*.

Many smaller billabongs and lagoons within Kakadu National Park have populations with apparent *N. kakaduensis* characteristics, including Island Billabong, Patonga Billabong, and Coonjimba Billabong (within the former Ranger Mineral leases) that were not sampled for molecular analyses. Additional occurrences of *Nymphaea* populations outside of Kakadu National Park from the "Top End" including Girraween Lagoon at Howard Springs, Manton Dam, and the wetlands at Humpty Doo deserve further analysis as possible occurrences of *N. kakaduensis*. A much broader survey of the northern wetlands of the Northern Territory along with the generation of molecular data for all taxa present at each location will provide a better understanding of geographical extent of *N. kakaduensis* and other species.

Taxonomic Treatment

Nymphaea kakaduensis C.B.Hellq., A.Leu & M.L.Moody, *sp. nov.*

Type: Australia: Northern Territory: Kakadu National Park, billabong at upper end of Jim Creek, SE of Rt. 21, west of Patonga Community, 12°57.676'S, 132°34.516'E, 29 April 2011, *C.B. Hellquist 17211, A. Leu*, and *F. Baird* (holotype: DNA; isotypes: BRIT, CNS, GH, NSW).

Perennial with a globose rhizome. Leaf blade oval–oval-elliptic, dark green above, dark purple below, 15.6–17.4 cm long, 11.8–16.6 cm wide; margins entire to sinuate-crenate to slightly undulate; petiole, green–brownish green, some streaked; stipules fused for c. 2 cm. Flower raised above the surface, fragrant. Sepals 3.0–6.0(–8.0) cm long, 1.0–2.6 cm wide, white, pink/brown or green above mostly flecked or streaked, apex acute-blunt or blunt. Petals usually white, occasionally blue, becoming pinkish or blue at apex. Petals 14–27(–36), 2–5 cm long, 0.6–2.0 cm wide, ovate–elliptic, some narrowing at base; apex blunt, obtuse, rounded, occasionally blunt-acute, flower shape is generally cupped, 5.5–10.5 cm wide (avg. 8.3 cm). No gap between petals and stamens. Stamens yellow, 80–200; anther length 3–10 mm; filament length 2–24 mm; carpels 14–30. Fruit globose, c. 2.0–4.0 cm diam; green at apex, sepals attached, seeds dark brown–dark olive, ovoid, with 1 longitudinal ridge; seed size avg. 2.0 (1.8–2.1) × 1.3 (1.2–1.3) mm, beak lacking or to 1.0 mm. (Figure 4)

Diagnostic characters: Differs from *N. violacea* by presence of smaller, mostly white flowers with upturned, blunt ovate–elliptic petals. Sepals and petals are often faintly pink-tipped and buds are blunt at the apex. Seeds are larger on average, 2.0 × 1.3 mm. The adaxial leaf surface is a darker green than in *N. violacea*.

Distribution: Currently only known from Kakadu National Park, in Jim Jim Creek and Billabong, Home Billabong, and Lake Jabiru. Probably in Island Billabong, Patonga Billabong, and Coonjimba Billabong, and the species may be more widespread in the Top End.

Ecology: The species grows in usually permanent billabongs. Recorded in association with *Nymphaea macrosperma*, *N. pubescens* and *N. violacea*.

Phenology: Flowering and fruiting recorded for April to June.

Specimens examined: NORTHERN TERRITORY: Kakadu National Park, billabong southwest of Home Billabong near Yellow Waters shore, 12°33.6918'S, 131°18.0747E', 28 April 2011. *C.B. Hellquist 17198*, *A. Leu, F. Baird & D. Miller* (BRIT, CAS, DNA, GH); Kakadu National Park, Jim Jim Billabong, 12°56'32"S, 132° 73.4743', 28 April 2011, *C.B. Hellquist 17202 & A. Leu, F. Baird & D. Miller* (CNS, DNA); Kakadu National Park, billabong at upper end of Jim Jim Creek, SE of Rt. 21, west of Patonga Community, 12°57.676'S, 132°34.516'E, 29 April 2011, *C.B. Hellquist 17212, A. Leu & F. Baird* (DNA, NSW); Kakadu National Park, Lake Jabiru, Jabiru, 12°40'26"S, 132°50'32"E, 15 June 2002, *S.W.L. Jacobs 8792 & C.B. Hellquist* (CNS, DNA, NSW); Kakadu National Park, Jim Jim Billabong, 12°56'32"S, 132°33'05"E, 17 June 2002, *S.W.L. Jacobs 8799 & C.B. Hellquist* (B, BRIT, NSW, PERTH); Kakadu National Park, Jim Jim Billabong, 12°56'32"S, 132°33'05, 17 June 2002, *S.W.L. Jacobs 8800 & C.B. Hellquist* (CNS, DNA, NSW).

Conservation status: Locally restricted on current knowledge, but protected within Kakadu National Park and not under immediate threat.

Etymology: The epithet refers to Kakadu National Park where the species occurs.

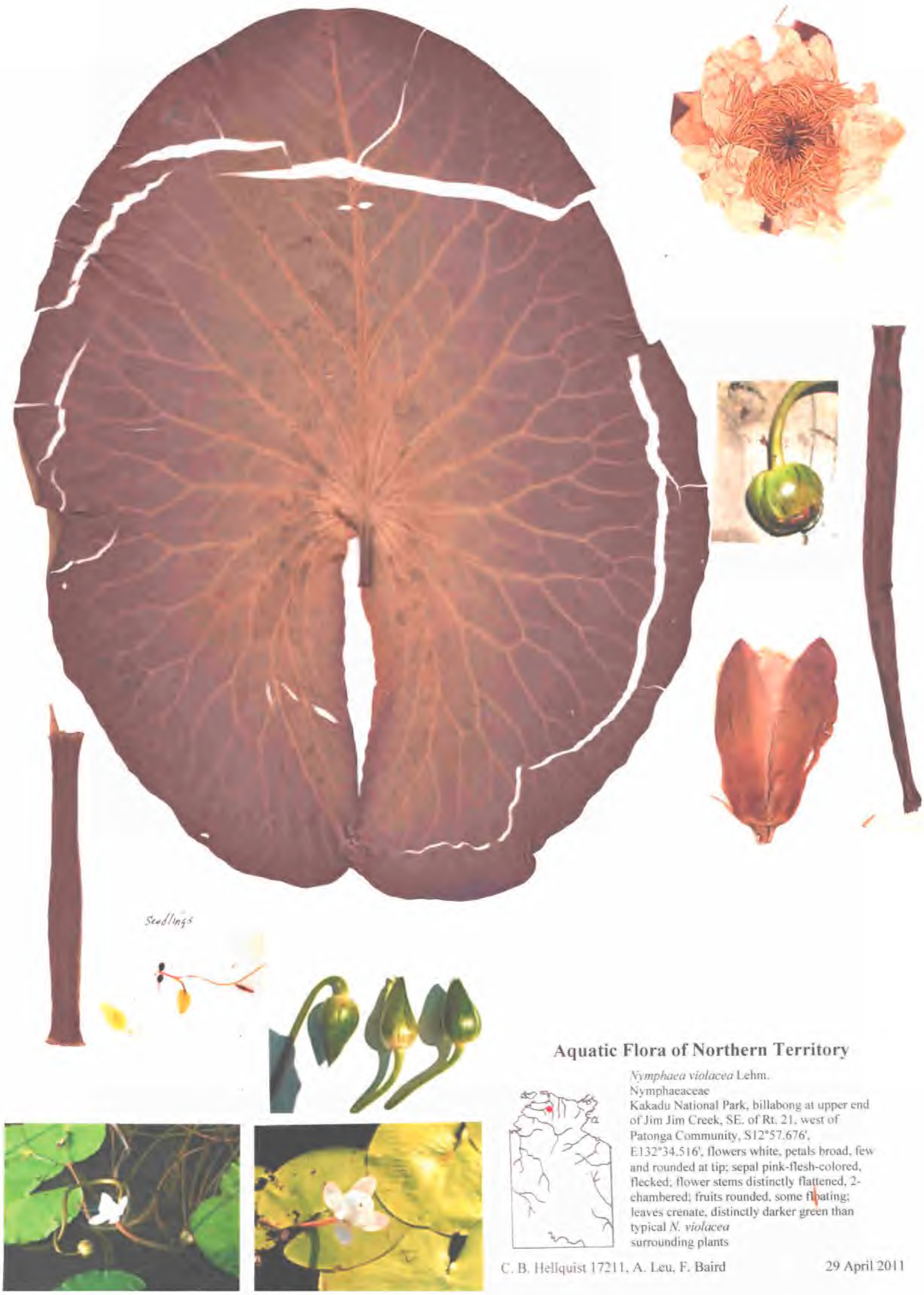

Fig. 4. Holotype: Australia: Northern Territory: Kakadu National Park, billabong at upper end of Jim Jim Creek, SE of Rt. 21, west of Patonga Community, 12°57.676'S, 132°34.516'E, 29 April 2011, *C.B. Hellquist* 17211, *A. Leu*, and *F. Baird*, (holotype: DNA)

Key to *Nymphaea* of Kakadu National Park and "Top End" coastal floodplains

1. Plants with distinct gap between petals and sepals 2
1: Plants with petals grading into stamens..... 3
2. Seeds 3–4.5 mm long, 2–3 mm wide; leaf margin toothed; flowers blue ..... ***N. macrosperma***
2: Seeds c. 0.75 mm diam; leaf margin entire to slightly sinuate; flowers white ..... ***N. nouchali***
3. Leaf margin dentate; leaf underside pubescent; flowers bloom at night until noon ..... ***N. pubescens***
3: Leaf margin entire or sinuate; leaf undersurface glabrous; flowers bloom during day..... 4
4. Seeds c. 1 mm diam., stamens 50–100; plants of seasonal shallow waters during wet season ..... ***N. hastifolia***
4: Seeds greater than 1 mm diam.; stamens 80–200; plants mostly of permanent waters..... 5
5. Flower petals oblanceolate with usually acute apex; flower buds acute at apex; seeds averaging 1.5 (1.4–2.0) ×1.0 (0.9–1.6) mm ..... ***N. violacea***
5: Flower petals ovate–elliptic with usually blunt apex; flower buds blunt at apex; seeds averaging 2.0 (1.8–2.1) × 1.3 (1.2–1.3) mm ..... ***N. kakaduensis***[1]

[1]All measurements obtained from specimens collected by S.W.L. Jacobs and/or C.B. Hellquist.

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References

Aston HI (1977) *Aquatic plants of Australia*. (Melbourne University Press, Melbourne)

Bączkiewicz A, Szczecińska M, Sawicki J, Stebel A, Buczkowska K (2017) DNA barcoding, ecology and geography of the cryptic species of *Aneura pinguis* and their relationships with *Aneura maxima* and *Aneura mirabilis* (Metzgeriales, Marchantiophyta). *PLoS One* 12: e0188837. http://doi.org/10.1371/journal.pone.0188837

Borsch T, Khidir XX, Wiersema JH, Löhne C, Barthlott W, Wilde V (2007) Phylogeny of *Nymphaea* (Nymphaeaceae): Evidence from substitutions and microstructural changes in the chloroplast *trn*T-*trn*F region. *International Journal of Plant Science* 168: 639–671. http://doi.org/10.1086/513476

Clement M, Posada DC, Crandall KA (2000) TCS: a computer program to estimate gene genealogies. *Molecular Ecology* 9: 1657–1659. http://doi.org/10.1046/j.1365-294x.2000.01020.x

Conard HS (1905) The waterlilies: a monograph of the genus *Nymphaea*. *Publications of the Carnegie Institutions of Washington* 4: 1–279.

Cowie ID, Short PS, Madsen MO (2000) *Floodplain Flora: a flora of the coastal floodplains of the Northern Territory, Australia: Flora of Australia Supplementary* Series 10. Environment Australia, Department of Environment and Heritage, Canberra.

Hollingsworth PM, Graham SW, Little DP (2011) Choosing and using a plant DNA barcode. *PloS One* 6: e19254. http://doi.org/10.1371/journal.pone.0019254

Jacobs, SWL (1992) New species, lectotypes and synonyms of Australasian *Nymphaea* (Nymphaeaceae). *Telopea* 4: 635–641. http://dx.doi.org/10.7751/telopea19814949

Jacobs SWL, Hellquist CB (2006) Three new species of *Nymphaea* (Nymphaeaceae) in Australia. *Telopea* 11: 155–160. http://dx.doi.org/10.7751/telopea20065719

Jacobs SWL, Hellquist CB (2011) New species, possible hybrids and intergrades in Australian *Nymphaea* (Nymphaeaceae) with a key to all species. *Telopea* 13: 233–243. http://dx.doi.org/10.7751/telopea20116016

Jacobs SWL, Porter CL (2007) Nymphaeaceae. In Wilson AJG (ed.) *Flora of Australia* vol. 2. Pp 259-275. (Australian Biological Resources Study, Canberra & CSIRO Publishing, Melbourne).

Liu J, Provan J, Gao LM, Li DZ (2012) Sampling strategy and potential utility of indels for DNA barcoding of closely related plant species: a case study in *Taxus*. *International Journal of Molecular Sciences* 13: 8740–8751. http://doi.org/10.3390/ijms13078740

Löhne C, Borsch T, Jacobs SWL, Hellquist CB, Wiersema J (2008) Nuclear and plastid DNA sequences reveal complex evolutionary patterns in Australian water-lilies (*Nymphaea* subgenus *Anecphya*, Nymphaeaceae). *Australian Systematic Botany* 21: 229–250. http://doi.org/10.1071/SB07010

Madison DR, Madison WP (2000) *MacClade, version 4.0*. (Sinauer, Sunderland)

Moody ML, Les DH (2010) Systematics of the aquatic angiosperm genus *Myriophyllum* (Haloragaceae). *Systematic Botany* 35: 121–139. http://doi.org/10.1600/036364410790862470

Moody ML, Palomino N, Weyl PS, Coetzee JA, Newman RM, Harms NE, Liu X, Thum RA (2016) Unraveling the biogeographic origins of the Eurasian watermilfoil (*Myriophyllum spicatum*) invasion in North America. *American Journal of Botany* 103: 709–718. http://doi.org/10.3732/ajb.1500476

Shaw J, Lickey EB, Beck JT, Farmer SB, Liu W, Miller J, Siripun KC, Winder CT, Schilling EE, Small RL (2005) The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *American Journal of Botany* 92: 142–166. http://doi.org/10.3732/ajb.92.1.142

Taberlet P, Gielly L, Pautou G, Bouvet J (1991) Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109. http://doi.org/10.1007/BF00037152

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Lechenaultia peregrina, a new species of Goodeniaceae from northern Australia, New Guinea and the Moluccas

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Abstract

Morphological studies of *Lechenaultia filiformis* R.Br. have determined that more than one taxon is presently included under that name. We here recognise the suite of disjunct populations from north-east Queensland, north-east Northern Territory, New Guinea and the Moluccas as a new species, *Lechenaultia peregrina* R.W.Jobson & R.L.Barrett. This is the third tropical species of *Lechenaultia* currently recognised, however further studies are required to assess the status of about five additional entities in the Northern Territory and Western Australia currently included in *L. filiformis s.l.* Seed article morphology is critical for species delimitation in tropical *Lechenaultia*, but seed articles are often absent from collections, or only immature, as they fall quickly once ripe.

Introduction

Lechenaultia R.Br. (Goodeniaceae) is near-endemic to Australia, with twenty one species endemic to southern Western Australia, one in south Australia, four species in central Australia, three species endemic to northern Australia, and one species extending to New Guinea and the Moluccas (Leenhouts 1957; Morrison 1987, 1992; Carolin 2007). The description of *Lechenaultia orchestris* K.A.Sheph. & Hislop (Shepherd and Hislop 2020) and our new species brings the number of named species in the genus to 30. A sister relationship of *Lechenaultia* to a clade that includes *Anthotium* R.Br. and *Dampiera* R.Br. has now been well-established (Gardner *et al.* 2016; Shepherd *et al.* 2020).

Lechenaultia filiformis R.Br. is the best known tropical species in the genus, though *L. agrostophylla* F.Muell. (Mueller 1867) was recognised as distinct until 1987, and that name had been more widely applied in northern Australia (Morrison 1987). Morrison (1988) described *L. ovata* Morrison as a highly localised species from the top end of the Northern Territory and Barrett and Barrett (2015) described *L. mimica* M.D.Barrett & R.L.Barrett from the West Kimberley. Further investigation of the *L. filiformis* complex is warranted as reassessment of specimens suggests it includes a number of morphologically and geographically distinct entities.

Brown (1810) included three collections in his concept of *Lechenaultia filiformis*, two from north Queensland, and one from the Northern Territory. *Lechenaultia filiformis* in the strict sense (as typified by Morrison 1987) is probably restricted to the eastern Northern Territory and extending just over the border into Queensland

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around the Gulf of Carpentaria. The lectotype morphotype is an annual with ± filiform leaves and flowers with relatively long sepals, but relatively small corollas. A second form is partially sympatric with *L. filiformis* in the Borroloola region [here recognised as *L.* sp. Borroloola (T.S.Henshall 2671)], differing in being a perennial with ± flat leaves and flowers with relatively short sepals, but very large corollas. The proximity of two taxa near the type location has probably confounded previous attempts to understand morphological variation in the complex. There are additional forms across the top end of the Northern Territory and Kimberley region of Western Australia, one of which corresponds to the type of *L. agrostophylla*, however detailed morphological studies are required to determine species limits in *L. filiformis s. lat*. *Lechenaultia* sp. Liverpool River (K.G. Brennan 7959), apparently allied to *L. ovata*, also requires resolution but appears to quite a distinctive entity (Barrett and Barrett 2015; K. Brennan, pers. comm.).

In assessing variation in *L. filiformis* s. lat., it is recommended that the following characters be critically examined: 1. Plants annual or with a distinctly perennial rootstock; 2. Plant habit (erect, spreading, ascending, decumbent, prostrate); 3. Leaf shape in section at midpoint (and general dimensions); 4. Leaves reducing in size up the stem or similar throughout; 5. Proportion of fruit developing articles; 6. Length of most sepals and relative length of longest sepal; 7. Corolla tube length; 8. Corolla total length; 9. Corolla wing shape on adaxial and abaxial petals; 10. Corolla colour; 11. Corolla aspect from side view; 12. Nature of tactile (pollination) guides (see Carolin 1959, 1960). 13. Article shape and size. Variation in article characteristics may be particularly diagnostic (see Carolin 1966; Morrison 1988; Barrett and Barrett 2015 for illustrations and descriptive notes).

A taxon from the Northern Territory that was initially thought to be only known from a single collection, *Lechenaultia* sp. Gove (K.G. Brennan 7684), has now been shown to match material from north-east Queensland, New Guinea and the Moluccas, all previously included under *L. filiformis* (and the only taxon within this range). Examination of a larger range of specimens has enabled a clear concept to be defined and it is readily distinguished from the typical form of *L. filiformis*. We here describe it as a new species, *Lechenaultia peregrina*, following observation in the field by RWJ and critical examination of specimens.

The new species is well represented by collections, going back to a collection by Banks and Solander from the Endeavour River in 1770. It was illustrated for Banks' only recently published Florilegium (Banks 1982: Plate 176) and by Bailey (1913: 282, Fig. 250). Brown's original description of *L. filiformis* included specimens from both Queensland and the Northern Territory, so encompassed both *L. filiformis* and *L. peregrina* as defined here, but Morrison (1987: 21) chose Brown's collection from North Island, in the Gulf of Carpentaria, as the lectotype for the species, assigning the name to the Gulf taxon. It is noteworthy that Bentham (1869: 44) maintained both *L. filiformis* and *L. agrostophylla* as distinct species, though with some reservations, and noted differences between the syntypes of *L. filiformis* from the Northern Territory and Queensland. Bentham's assessment was hampered by limited material to determine the extent of variation between populations and regions, a situation which can now be addressed. Both *L. filiformis* and *L. agrostophylla* were maintained as distinct species until *L. agrostophylla* was included as a synonym of *L. filiformis* by Morrison (1987). It is likely that future studies will reinstate *L. agrostophylla* for an entity in the western Northern Territory and eastern Kimberley, as Morrison (1987) typified the name on a specimen from the upper Victoria River.

Key to tropical, annual (or occasionally short-lived perennial) species of *Lechenaultia* (modified from Barrett and Barrett 2015)

1. Plants decumbent. Leaves lanceolate to narrowly elliptic, 1.5–5 mm wide. Articles 0.7–1.4 mm long, short-oblong to elliptic, less than twice as long as wide..... **2**

1: Plants ascending to erect. Leaves filiform to linear or very narrowly lanceolate, up to 41 mm long, up to 2.1(–3.0) mm wide. Articles 2.0 mm or longer, elongate and irregularly cylindrical or irregular in shape, more than twice as long as wide..... **3**

2. Corolla 9–14 mm long when dry, rich mauve on lobes with a broad yellow throat, a white line separating the colours. Articles grey, 0.7–1.3 mm long, a short-oblong plate with an oblong 'cushion' (lifting at each end) on each 'face', food bodies absent..... ***L.* sp. Liverpool River (K.G. Brennan 7959)**

2: Corolla 5.5–8(–10) mm long when dry, white, pale mauve or pale mauve with yellow palate. Articles reddish-brown, 1.0–1.4 mm long, oblong-elliptic with rounded corners, main plane a raised pale rim, each 'face' with two raised areas joined by a rib, with pale food bodies in pockets on one side..... ***L. ovata***

3. Corolla 9.5–19 mm long, pale mauve with a white throat, lacking any yellow markings. Articles simple, elongate and irregularly cylindrical, with a low, elongate furrow on each side ..... ***L. mimica***

3: Corolla 9.5–25 mm long, usually either rich dark purple, pale mauve, pinkish or white, with yellow markings. Articles complex, in side-view consisting of a thin plate with a 'cushion' on each face, each cushion raised to a thick diverging short spur at each end, to create a ±trilobed apex at each end **4**

4. Corolla pale mauve, pinkish or white, 9.5–13 mm long. Longest adaxial sepal 2.5–5.1 mm long. Articles 1.9–2.3 mm long, with a central depression that has a regularly cracked pattern, the whole 'cushion' is surrounded by a raised rim. Perennial (thinly woody at base and with a thin rhizome). Wet boggy sand in seasonal swamps and in grasslands ..... ***L. peregrina***

4: Corolla usually rich dark blue–purple with thin bright yellow stripes on palate, 13.5–25 mm long (dry). Longest adaxial sepal up to 8.5 mm long. Article 'cushions' not depressed nor cracked, 2.9–3.3 mm long. Annual or perennial. Usually in non-waterlogged habitats ..... ***L. filiformis* s.l.**

Taxonomy

Lechenaultia peregrina R.W.Jobson & R.L.Barrett, *sp. nov.*

Type: Queensland: Olive River Environmental Reserve, 5 km E by road of 'Bromley' Homestead, 45 km E of Moreton Telegraph Station, Cape York Peninsula, 18 June 2007, *P.I. Forster PIF32817 & K.R. McDonald* (holo: NSW 921773; iso: BRI AQ0752787, (plus spirit material), MEL 2407327, MEL 2407328).

Lechenaultia sp. Gove (K.G. Brennan 7684), Barrett & Barrett (2015: 479)

Erect to spreading or ascending perennial herb to 40 cm high, with 1–21 primary branches, 11–60 cm long, spindly stems sometimes supported by other vegetation, glabrous except for subsessile glandular hairs clustered in the axil of the leaf base near the stem, sparse on the sepals, and various hairs on the corolla. Stems herbaceous, 0.9–1.8 mm diam., pale brown, bark not or scarcely developing, primary branches 0.6–0.8 mm diam., ±angular when dry with irregular, narrow translucent wings. Leaves alternate, scattered, erect to spreading, linear, 7–25 mm long, 0.4–0.6 mm wide, becoming somewhat reduced towards inflorescence, glabrous, margin entire (irregularly wrinkled when dry), base not constricted, apex subacute to acuminate; petiole usually not distinct, sometimes to 0.4 mm long. Inflorescences open, appearing to be terminal, monochasial cymes, with 1–3 distant flowers, with 1–3 leaves between each flower; bracts not differentiated from leaves. Peduncles 1.5–5.5 mm long. Sepals ±linear, unequal, narrowing to a fine point, adaxial sepal distinctly longer, 4.2–5.1 mm long, *c.* 0.5 mm wide, other sepals 1.8–3.5 mm long, *c.* 0.2 mm wide, glabrous. Corolla 10.5–14.5 mm long, pale mauve, pale pink or cream on lobes, becoming paler with age, and whitish to cream in throat of adaxial surface, whitish to cream on abaxial surface, long slit on adaxial side almost to base; glabrous outside, with dense, soft, sinuous simple hairs 0.3–0.5 mm long on the inside margins of the adaxial lobes matting together, shorter, simple, ±straight hairs 0.1–0.3 mm long moderately dense inside throat and sometimes extending to wing margins; throat white inside; lobes unequal in length, adaxial lobes united with lower lobes in basal 3.3–4.1 mm, otherwise free to base, free part of adaxial lobes 5.3–6.8 mm long, held in line with united part of abaxial lobes for the length of the indusium, then spreading-erect, inner wing reduced or absent, outer wings 0.7–0.9 mm wide, apex usually with 3 blunt teeth; abaxial three lobes united in basal 6.5–8.2 mm (inner surface with dense rows of hairs 0.1–0.3 mm long), lobes 2.7–5.2 mm long, both wings running full length of lobes, sometimes apex exceeding the lobes by up to 0.4 mm, 0.3–0.8 mm wide, obtuse to subacute, margins weakly erose to entire. Stamens with filaments 1.6–2.4 mm long; anthers 0.8–1.0 mm long, *c.* 0.3 mm wide. Pollen pale yellow, ovoid, *c.* 0.1 mm long, *c.* 0.05 mm diam., Style 6.0–7.9 mm long, glabrous except for a patch of subsessile glandular hairs, *c.* 0.05 mm long on rear of indusium, basal part mostly hidden within corolla tube; indusium broader than long, 0.8–0.9 mm long, 1.1–1.4 mm wide, with subsessile glandular hairs above, dense short bristles 0.1–0.3 mm long on lips, mouth gaping. Ovary 15–28 mm long, ±linear, glabrous. Fruit 24–31 mm long (not including retained sepals), articles 5–9 opposite to subopposite pairs, seeds usually developing only in lower two thirds of fruit. Articles cream to dull brown, 1.9–2.3 mm long, 0.7–0.8 mm wide, ±pentangular in section, abaxial surface (against the placental axis) ±flat with distinct but with very narrow 'wings', glabrous; adaxial surface with a raised, central ridge sloping to the 'wings', in places ±roughened with friable material, lateral 'cushions' have a central depression that has a regularly cracked pattern and the whole 'cushion' is surrounded by a slightly raised rim. Figure 1.

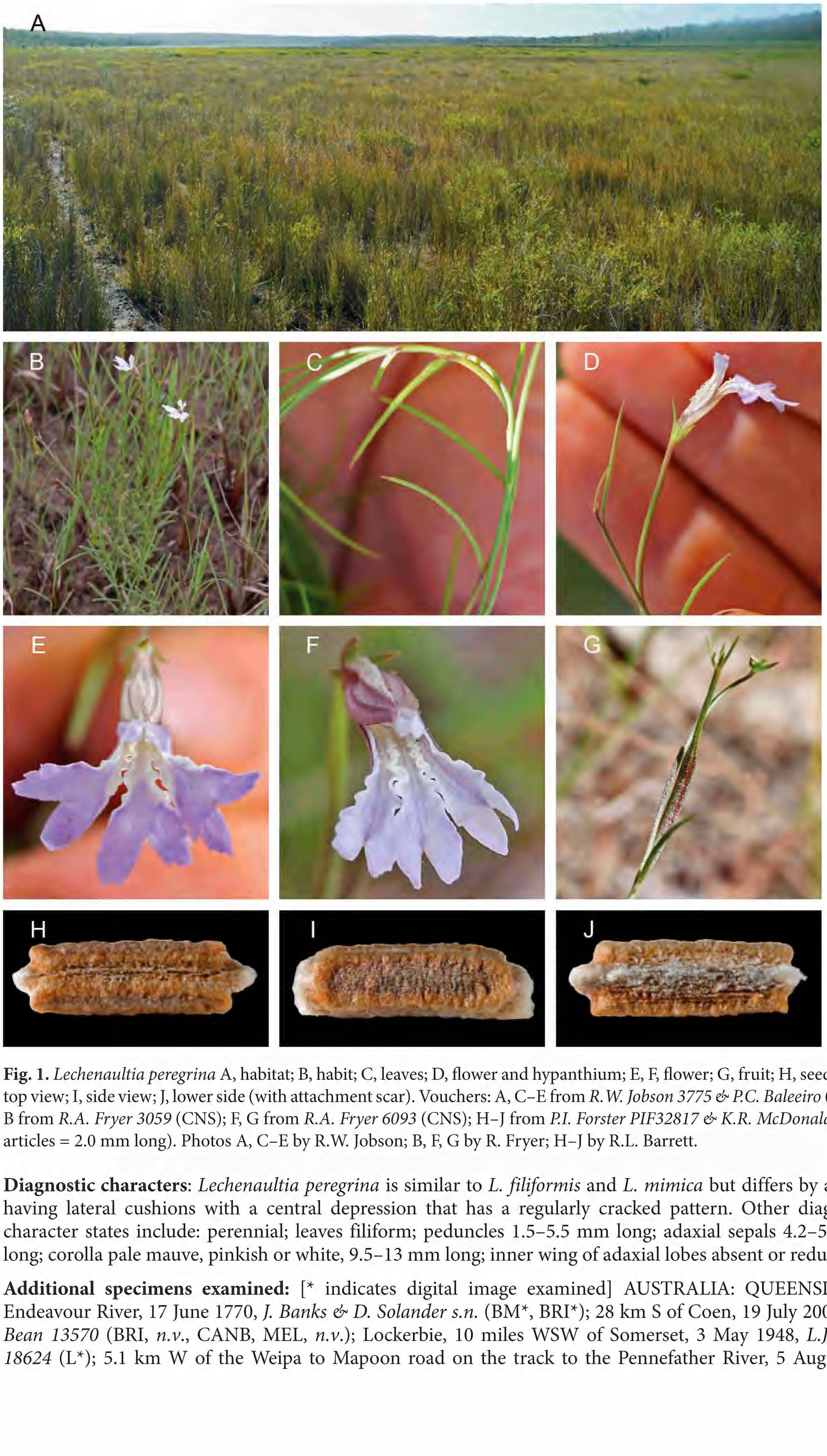

Fig. 1. *Lechenaultia peregrina* A, habitat; B, habit; C, leaves; D, flower and hypanthium; E, F, flower; G, fruit; H, seed article top view; I, side view; J, lower side (with attachment scar). Vouchers: A, C–E from *R.W. Jobson 3775 & P.C. Baleeiro* (NSW); B from *R.A. Fryer 3059* (CNS); F, G from *R.A. Fryer 6093* (CNS); H–J from *P.I. Forster PIF32817 & K.R. McDonald*. (Seed articles = 2.0 mm long). Photos A, C–E by R.W. Jobson; B, F, G by R. Fryer; H–J by R.L. Barrett.

Diagnostic characters: *Lechenaultia peregrina* is similar to *L. filiformis* and *L. mimica* but differs by articles having lateral cushions with a central depression that has a regularly cracked pattern. Other diagnostic character states include: perennial; leaves filiform; peduncles 1.5–5.5 mm long; adaxial sepals 4.2–5.1 mm long; corolla pale mauve, pinkish or white, 9.5–13 mm long; inner wing of adaxial lobes absent or reduced.

Additional specimens examined: [* indicates digital image examined] AUSTRALIA: QUEENSLAND: Endeavour River, 17 June 1770, *J. Banks & D. Solander s.n.* (BM*, BRI*); 28 km S of Coen, 19 July 2008, *A.R Bean 13570* (BRI, *n.v.*, CANB, MEL, *n.v.*); Lockerbie, 10 miles WSW of Somerset, 3 May 1948, *L.J. Brass 18624* (L*); 5.1 km W of the Weipa to Mapoon road on the track to the Pennefather River, 5 Aug. 1983,

J.R. Clarkson 4903 (BRI, *n.v.*, MBA, *n.v.*, NSW, QRS, *n.v.*, PERTH); 1.6 km S of The Wenlock River on The Peninsula Development Road, 20 Apr. 1990, *J.R. Clarkson 8400 & V.J. Nelder* (BRI, *n.v.*, L*, MBA, *n.v.*, NSW, QRS, *n.v.*); Nicholson Road, Cardwell, North Queensland, 25 April 2017, *R.A. Fryer 6093* (CNS*); Cape Bedford Rd, Hopevale, North Queensland, 30 March 2015, *R.A. Fryer & J. Newland 3059* (CNS*); Track into N Jardine River campsites, *c.* 42 km S of Injinoo, 10 June 2016, *R.A. Fryer 2133* (CNS*); *c.* 4.3 km S of Cape York tip, 43 m, 21 July 2019, *R.W. Jobson 3775 & P.C. Baleeiro* (BRI, NSW); N of Cholmondeley Creek Crossing on Telegraph Line road, 6 Mar. 1992, *R.W. Johnson 5140* (AD, *n.v.*, BRI, *n.v.*, DNA, *n.v.*, MEL, *n.v.*, NSW); Bruce Highway - Nicholson Road junction at start of old track on road verge, 21 Sept. 2016, *R.W. Purdie 10892* (CANB); Moa Island, Torres Strait, 14 May 2003, *B.S. Wannan, 2922 & I.T. Toh* (BRI, *n.v.*, NSW).

NORTHERN TERRITORY: Gove, Lethram River, 20 May 2008, *K.G. Brennan 7684* (DNA*).

PAPUA NEW GUINEA: West Poit, Sudest Island, Milne Bay District, 8 Nov. 1965, *E.E. Henty NGF 27117* (BRI, *n.v.*, L*); Sibidiri, Mai Kussa River, Morehead subdist., Western District, Papua, 11 July 1968, *E.E. Henty & P. Katik, NGF 38778* (A, *n.v.*, BRI, *n.v.*, CANB, L*); *c.* 15 miles N. of Morehead Patrol Post, Western District, 19 Aug. 1967, *R. Pullen 7108* (CANB, L*); *c.* 1 mile S. of Morehead Patrol Post along track to Tonda, Western District, 23 Aug. 1967, *R. Pullen 7137* (CANB, L*).

INDONESIA: North East Kepala Burung, Irian Jaya, Kabupaten Manokwari; Kecamatan Kebar. Bukit Sintiri, between Sungai apriri, between Sungai Apriri and Sungai Aremi, 11 May 1994, *M.J.S. Sands & M. Jitmau 6545* (A, AA, BISH, BO, CANB, K, L*, LAE, MAN, P, SING [all *n.v.* except L]); New Guinea; Singgi, District Jafi Afd, Hollandia, 13 Feb. 1957, *F.A.W. Schram 2867* (L*); Aru Islands: Palau Trangan, Meme, 15 Apr. 1993, *M. M.J. van Balgooy & J.A.B. Mamesah 6299* (L*, NSW); Aru Islands: Palau Trangan, between Sia and Beltubun, 27 Oct. 1994, *M.M.J. van Balgooy 6712* (L*); Vogelkop Peninsula, Kebar valley, above Aremi village, opposite Andjai, 13 Dec. 1961, *P. van Royen 8248* (A, BO, CANB, K, L*, LAE, RSA [all *n.v.* except L]).

Etymology: The specific epithet is from the Latin *peregrinus* (from foreign parts, foreign, or exotic; also used by Brown (1956) for 'travelling about', but probably derived from *peregrinor*) and refers to the disjunct distribution of this species, which is the only *Lechenaultia* to have dispersed outside of Australia.

Distribution and Ecology: Reasonably widespread on the eastern side of Cape York Peninsula, from Townsville north to Badu and Moa Islands in the Torres Strait, and the Mibini District in southern Papua New Guinea. Also recorded from Indonesian New Guinea Wassi Kussa, Kebar Valley) and in the southern Moluccas (Aru and Trangan Islands) (Leenhouts 1957). Commonly grows on plains where it is usually associated with seasonally waterlogged soils, especially sands or sandy loam. Grows in open woodlands or swampy sedgelands. Recorded in association with *Acacia crassicarpa*, *Allocasuarina littoralis*, *Alyxia spicata*, *Asteromyrtus brassii*, *Asteromyrtus lysicephala*, *Banksia dentata*, *Breynia stipitata*, *Byblis liniflora*, *Corymbia clarksoniana*, *Cyperus* sp., *Drosera lanata*, *Eriachne* sp., *Eriocaulon* sp., *Eucalyptus brassiana*, *Eucalyptus tetrodonta*, *Exocarpos latifolius*, *Goodenia mystrophylla*, *Goodenia pilosa*, *Grevillea pteridifolia*, *Ischaemum australe* var. *australe*, *Leptocarpus schultzii*, *Leucopogon yorkensis*, *Livistona muelleri*, *Lomandra banksii*, *Lophostemon suaveolens*, *Melaleuca quinquenervia*, *Melaleuca viridiflora*, *Mitrasacme pygmaea*, *Pandanus solms-laubachii*, *Pandanus tectorius*, *Rhynchospora* spp., *Schoenus melanostachys*, *Stylidium alsinoides*, *Tricoryne anceps*, *Utricularia caerulea*, *Xanthorrhoea johnsonii* and *Xyris* sp.

Phenology: Flowering and fruiting recorded for March to July in Australia, but as early as November in New Guinea.

Conservation status: *Lechenaultia peregrina* is relatively widespread and is not considered threatened, though it is relatively poorly collected outside of Queensland.

Notes: This species has been well-collected, but its taxonomic status has been overlooked due to minimal regional comparative studies in tropical Australian herbs with localised species often going unrecognised (e.g. Baleeiro *et al.* 2020). The small sepals are similar to *L. mimica*, suggesting that these species may be more closely related to each other than to *L. filiformis* s. str.

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References

Bailey FM (1913) *Comprehensive catalogue of Queensland plants* (Government Printer, Brisbane) https://www.biodiversitylibrary.org/item/123358#page/307/mode/1up

Baleeiro PC, Jobson RW, Barrett RL (2020) *Drosera stipularis*, a new species for the *Drosera petiolaris* complex from Cape York Peninsula, Queensland. *Telopea* 23: 35–40. https://dx.doi.org/10.7751/telopea14200

Banks J (1982) *Banks Florilegium, Part 8, Plate 176*. Lechenaultia filiformis (*Goodeniaceae*). (Alecto Historical Editions, Salisbury, UK)

Barrett RL, Barrett MD (2015) Four new species of Goodeniaceae from Western Australia, including the smallest species in the family, a putative seed-article elaiosome and possible floral mimicry in *Lechenaultia*. *Australian Systematic Botany* 27: 469–482. https://doi.org/10.1071/SB14035

Bentham G (1869) *Flora australiensis: a description of the plants of the Australian territory. Volume 4*. (L.Reeve, London) https://www.biodiversitylibrary.org/page/26123366#page/60/mode/1up

Brown R (1810) *Prodromus florae Novae Hollandiae et insulae Van-Diemen, exhibens characters plantarum quas annis 1802–1805*: 586–587. (Taylor & Socii, Londini) https://doi.org/10.5962/bhl.title.3678

Brown RW (1956) *Composition of scientific words. A manual of methods and a lexicon of materials for the practice of logotechnics* (Smithsonian Books, Washington)

Carolin RC (1959) Floral structure and anatomy of the Family Goodeniaceae Dumort. *Proceedings of the Linnean Society of New South Wales* 84: 242–255. https://www.biodiversitylibrary.org/item/108624#page/258/mode/1up

Carolin RC (1960) The structures involved in the presentation of pollen to visiting insects in the order Campanulales. *Proceedings of the Linnean Society of New South Wales* 85: 197–207. https://www.biodiversitylibrary.org/item/134852#page/709/mode/1up

Carolin RC (1966) Seeds and fruit of the Goodeniaceae. *Proceedings of the Linnean Society of New South Wales* 91: 58–83. https://www.biodiversitylibrary.org/item/108606#page/68/mode/1up

Carolin RC (2007) Goodeniaceae. In: Kadereit JW, Jeffrey C (Eds) *The Families and Genera of Vascular Plants Vol. VIII: Asterales*. pp. 589–590. (Springer, Cham) https://doi.org/10.1007/978-3-540-31051-8_8

Gardner AG, Sessa EB, Michener P, Johnson E, Shepherd KA, Howarth DG, Jabaily RS (2016) Utilizing next-generation sequencing to resolve the backbone of the Core Goodeniaceae and inform future taxonomic and floral form studies. *Molecular Phylogenetics and Evolution* 94: 605–617. https://doi.org/10.1016/j.ympev.2015.10.003

Leenhouts P (1957) Goodeniaceae. In: Steenis CGGJ van (Ed.) *Flora Malesiana ser. 1, 5*. pp. 335–344. (Nordhoff, Djakata)

Morrison DA (1987) Taxonomic and nomenclatural notes on *Lechenaultia* R.Br. (Goodeniaceae). *Brunonia* 9: 1–28. https://doi.org/10.1071/BRU9860001

Morrison DA (1988) Notes on the fruits of *Lechenaultia* (Goodeniaceae), with a new species from northern Australia. *Telopea* 3: 159–166. https://dx.doi.org/10.7751/telopea19884804

Morrison DA (1992) *Lechenaultia*. In George AS (ed.) *Flora of Australia. Vol. 35. Goodeniaceae, Brunoniaceae.* pp. 17–34. (Australian Government Publishing Service, Canberra)

Mueller FJH von (1867) *Fragmenta Phytographiae Australiae*. Vol. 6(41) (Government Printer, Melbourne) https://www.biodiversitylibrary.org/item/7223#page/9/mode/1up

Shepherd KA, Hislop M (2020) Dancing Lechenaultia (*Lechenaultia orchestris*, Goodeniaceae), a new species with horticultural potential from southern Western Australia. *Nuytsia* 31: 15–18. https://florabase.dpaw.wa.gov.au/science/nuytsia/938.pdf

Shepherd KA, Lepschi BJ, Johnson EA, Gardner AG, Sessa EB, Jabaily RS (2020) The concluding chapter: recircumscription of *Goodenia* (Goodeniaceae) to include four allied genera with an updated infrageneric classification. *PhytoKeys* 152: 27–104. https://doi.org/10.3897/phytokeys.152.49604

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Hiding in plain sight, *Ficus desertorum* (Moraceae), a new species of rock fig for Central Australia

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Abstract

A new species of lithophytic fig, *Ficus desertorum* B.C.Wilde & R.L.Barrett, endemic to arid Central Australia, is described and illustrated. It is distinguished from other species in *Ficus* section *Malvanthera* Corner by having stiff lanceolate, dark green, discolorous leaves; many parallel, often obscure lateral veins; petioles that are continuous with the midrib; with minute, usually white hairs and non- or slightly sunken intercostal regions on the lower surface. Previously included under broad concepts of either *Ficus platypoda* (Miq.) Miq. or *Ficus brachypoda* (Miq.) Miq., this species has a scattered distribution throughout Central Australia on rocky outcrops, jump-ups (mesas) and around waterholes. This culturally significant plant, colloquially referred to as the desert fig, grows on elevated landscapes in central Australia, including Uluru (Ayers Rock), Kata Tjuṯa (The Olgas) and Karlu Karlu (Devils Marbles), three of Central Australia's best-known natural landmarks. Evidence is provided to show these plants are geographically and morphologically distinct from *Ficus brachypoda*, justifying the recognition of *F. desertorum* as a new species. Taxonomic issues with *F. brachypoda* and *F. atricha* D.J.Dixon are also discussed. Lectotypes are selected for *Urostigma platypodum* forma *glabrior* Miq. and *Ficus platypoda* var. *minor* Benth.

Introduction

Figs are a globally recognisable and highly culturally significant plants. Figs are significant as objects of human spirituality, as major structural components of natural ecosystems providing both habitats and food, and they are dependent on elaborate mutualisms with wasps in the family Agaonidae for pollination (Wilson and Wilson 2013). Around two thirds of the world's 750 fig species are found in Asia and Australasia (Berg and Corner 2005). Australia is relatively poorly represented, with about 43 native species (Atlas of Living Australia 2020), but has a remarkable radiation of species into seasonally arid and arid environments (Dixon 2001a; Bruun-Lund 2019). Figs are a very important plant group for Australian Aboriginal people, providing critical resources, especially in more arid environments where seasonal availability of food becomes most critical, recorded in a considerable body of literature (Kemp 1891; Cleland 1932; Cleland and Johnston 1933, 1937, 1939; Tindale 1941, 1981; Johnstone and Cleland 1943; Sweeney 1947; Mountford 1950, 1962; Cleland and Tindale 1954, 1959; Meggitt 1957; Maconochie 1970; Latz and Griffin 1978; O'Connell *et al.* 1983; Nash 1984, 1993; Low 1991; Latz 1995, 2007; Brand-Miller and Holt 1998; Everard *et al.* 2002; Clarke 2007, 2008, 2012).

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The most recent treatments or summaries of Australian *Ficus* that cover most species are those by Corner (1965) and Chew (1989). More recent papers have only dealt with select species groups. The rock figs of northern and central Australia (*Ficus* section *Malvanthera* Corner) have been, and continue to be, difficult for taxonomists to circumscribe (Chew 1989; Henderson 1993; Dixon 1999, 2001a, 2002, 2003; Dixon *et al.* 2001). Many species occur in remote, poorly botanically explored locations across the rocky ranges of northern and inland Australia, are poorly represented in herbarium collections, and commonly display considerable morphological variation. Delimitation of species based primarily on herbarium specimens has remained challenging and a classification reflecting diversity observable in the field is yet to be achieved.

Following the taxonomic revision and determination of specimens by Dixon (2001a), the most frequently collected species of fig for north, west and central Australia is a broadly defined *Ficus brachypoda*.

Dixon (2001a) used two key features to distinguish *F. brachypoda*; plants with parts being variously hairy, and the intercostal [regions] not strongly sunken. Following Dixon's (2001a) taxonomic concepts, these two characters allow nearly any hairy Australian fig to be included in *F. brachypoda*, resulting in a highly morphologically variable species concept (Fig. 1). This is also reflected by the wide distribution of the species, from western Queensland, Northern Territory, northern Western Australia and northern South Australia. Dixon (2003) later also included collections from the Lesser Sunda Islands and Timor within this species. Thus defined, *Ficus brachypoda* is the most widely distributed of all Australian figs (Fig. 2A) and sympatric with five other figs in section *Malvanthera* Corner; *F. atricha* D.J.Dixon (2001a) (Fig. 2B), *F. cerasicarpa* D.J.Dixon (2001a), *F. lilliputiana* D.J.Dixon (2001b), *F. platypoda* (Miq.) Miq. (Miquel 1867–8) and *F. subpuberula* Corner (1960).

Considerable morphological variation can be seen in Herbarium collections of *F. brachypoda sensu* Dixon (2001a). Plants with large, almost glabrous, heart-shaped leaves (Fig. 1 A), others with small, obviously hairy, elongated leaves (Fig. 1 B), and much variation in between, are currently assigned to this species. Geographically, the concept includes populations spanning from the wet tropical north (>1400 mm rainfall p/a), to the arid interior of Australia (<250 mm rainfall p/a). At the time of writing, more collections were attributed to *F. brachypoda* (1522) than all five other north-west species in section *Malvanthera* combined: *F. atricha* (359), *F. cerasicarpa* (311), *F. lilliputiana* (71), *F. platypoda* (476), *F. subpuberula* (194); totalling 1411 records (Atlas of Living Australia, 14 Jan. 2020; http://www.ala.org.au).

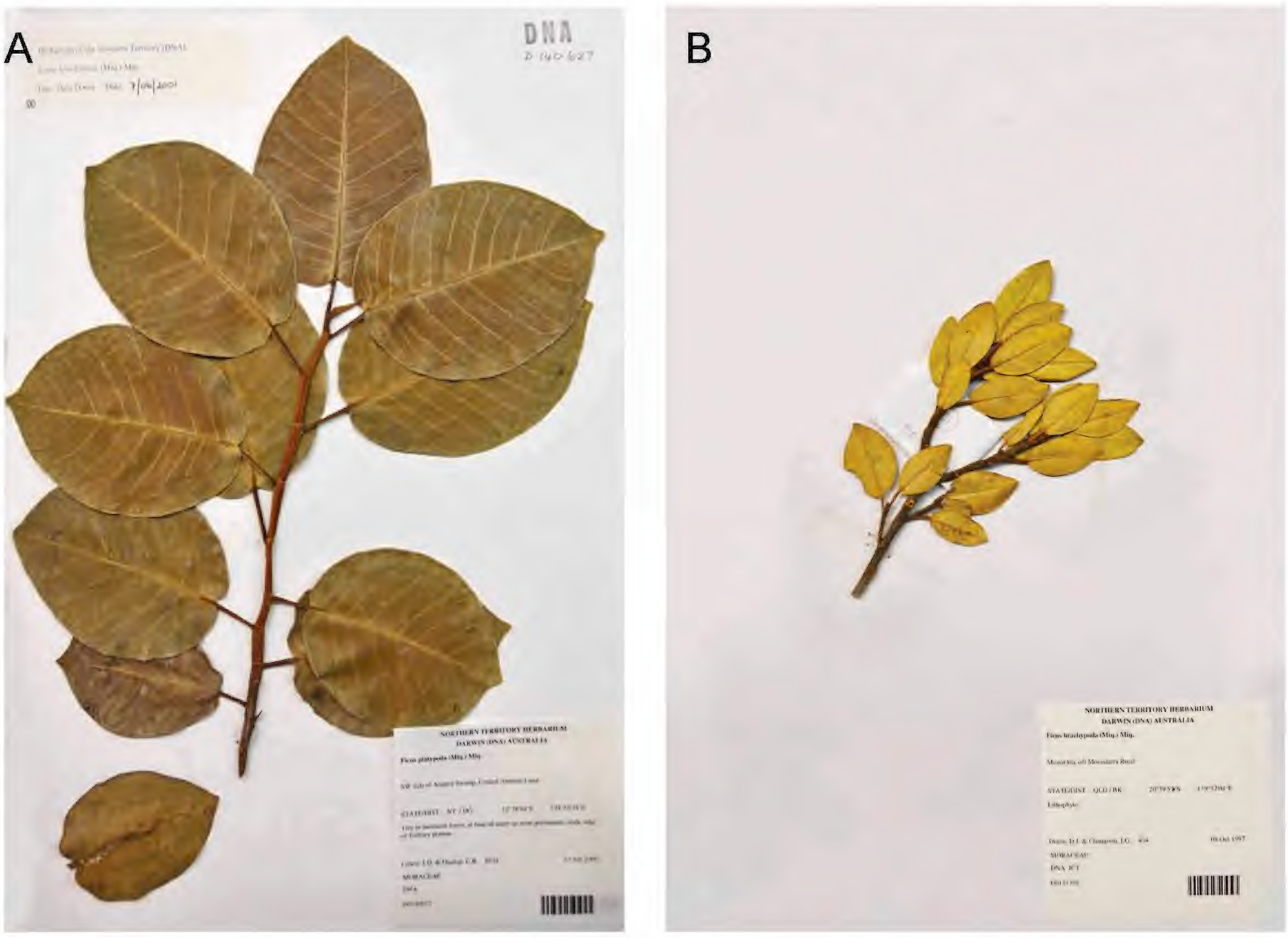

Fig. 1. Two specimens that have been determined by D.J. Dixon as *Ficus brachypoda.* A: From tropical Northern Territory; with large leaves and obvious veins (DNA D0140627). B: From western Queensland; with small narrow hairy leaves and barely visible veins (DNA D0151398). The right-hand collection is allied to *F. cerasicarpa*.

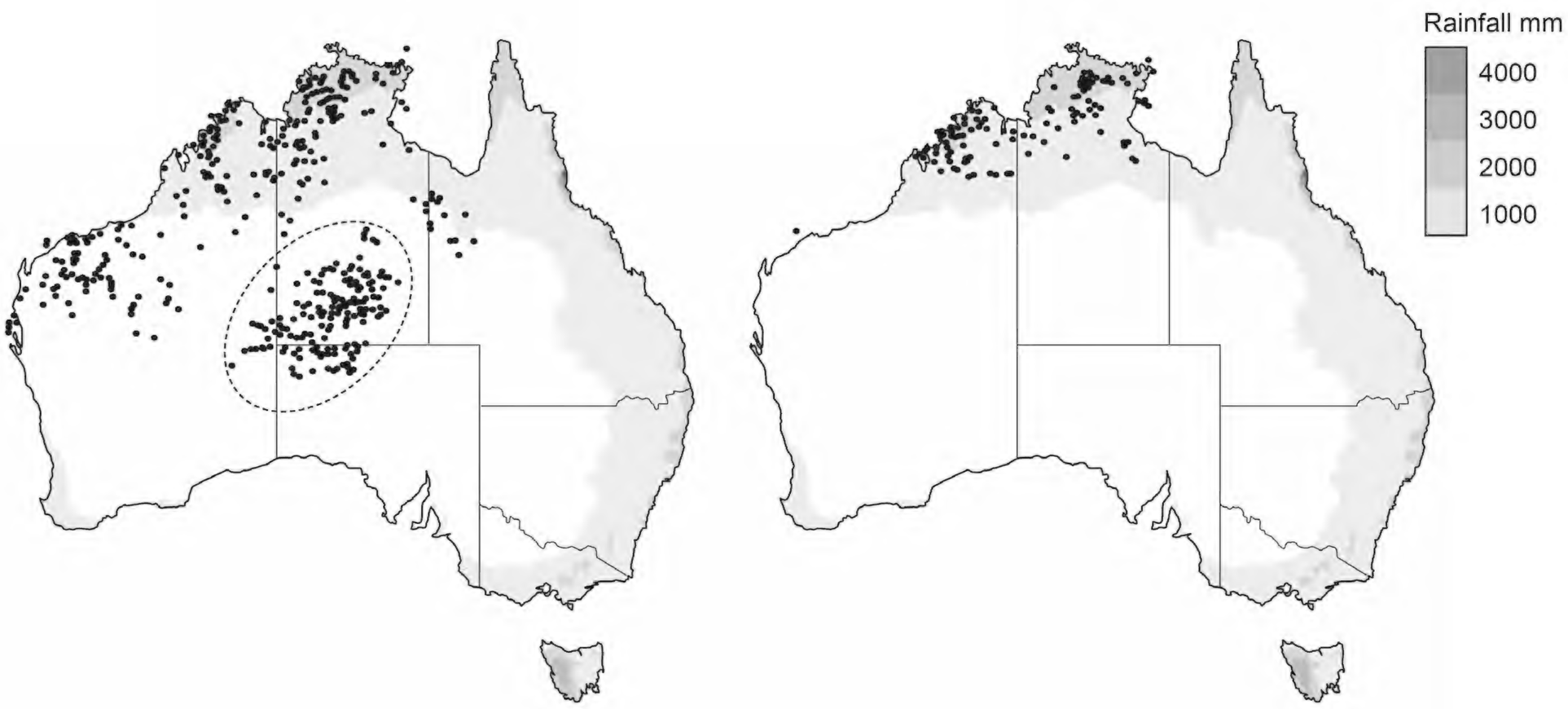

Fig. 2. The '*Ficus. brachypoda*' complex showing all collections for A: *F. brachypoda* (dashed ellipse covers specimens here separated as *F. desertorum*) and B: *F. atricha*. Map shows annual precipitation from bioclim12 (http://www.worldclim.oeg/bioclim) averaged over the period 1983–2012. Occurrence records downloaded from Atlas of Living Australia (http://www.ala.org.au). Accessed 22 January 2020.

The type specimen of *Ficus bachypoda* was collected from York Sound on the north coast of Western Australia by the French expedition of 1800–1803 to map the coastline of New Holland, led by Nicolas Baudin. Specimens from the vicinity (<100 km) of the type location are illustrated in Fig. 3.

Ficus brachypoda was included as a synonym of *F. obliqua* var. *puberula* (Benth.) Corner by Chew (1989), but Dixon (2001a) reinstated the species, and considerably altered the concept of *F. platypoda* at the same time. Dixon (2001a) reinstated *F. brachypoda* based on measurement of 25 morphological characters from 133 herbarium specimens. The 133 specimens were split into 2 groups based on unexplained gross morphology; the '*F. platypoda* complex' and '*F. leucotricha* complex'. The 2 datasets, containing mixed, variable morphotypes, missing data and multiple correlated variables, were log-10 transformed, an Euclidean distance matrix was created and presented as UPGMA (unweighted pair group method with arithmetic mean) dendrograms. Dixon found that both the '*F. platypoda* complex' and '*F. leucotricha* complex' further divided into 2 sub-groups.

Table 1. Dixon's (2001a) divisions of *F. platypoda* and *F. leucotricha* complexes into 4 species. The decision to not use the species name *F. platypoda* for specimens in the *F. platypoda* complex is explained in the nomenclatural notes of Dixon (2001a).

Complex	Group	Delimiter	Species
F. platypoda	*A*	variously hairy	*F. brachypoda*
F. platypoda	*B*	all parts hairless	*F. atricha*
F. leucotricha	*A*	syconia bracts 2.5–7.8 mm	*F. cerasicarpa*
F. leucotricha	*B*	syconia bracts 6.6–28.5 mm	*F. platypoda*

Six hair variables were found to be the main delimiting factors for the '*F. platypoda complex*', with the following characters responsible for the division with coefficient values of 0.85 or greater from UPGMA; Leaf pubescence abaxial surface (0.94); Fig pubescence (0.93); Leaf petiole pubescence (0.91); Young stem pubescence (0.90); Stipule pubescence (0.90); Leaf pubescence adaxial surface (0.90); and Leaf width (0.89). Though differences among the groups were statistically significant, there is no practical significance (Kirk, 1996) for taxonomic recognition of these groups. The division of Dixon's '*F. platypoda* complex' into the two species *F. brachypoda* and *F. atricha* based on the presence of hairs is too general to categorise the scope of variation found within the complex. Further, populations of morphologically distinct central Australian figs, which have, among other differences, narrower leaves compared to the tropical figs, were grouped with *F. brachypoda*. It is clear from examining herbarium specimens and from field work that *F. brachypoda* and *F. atricha* as defined by Dixon (2001a) represent unresolved species complexes needing further investigation. With the two species complexes growing intermixed at some locations and no practical delimiting characters, the two species are treated herein as the '*F. brachypoda* complex'.

Fig. 3. *Ficus brachypoda* specimens from the vicinity of the type location in the north-west Kimberley. A: small plant from the Artesian Range. B. lower surface of leaves showing sunken intercostal regions (left), and smooth upper surface (right). C: fruiting stem and petioles with characteristic hairs. D: branchlet apex with fruit and apical bracts with characteristic hairs. E: fruiting branchlet with floral bracts. F. longitudinal section of fruit. Voucher: B–F from Boongaree Island, *P.G. Wilson 11395* (CANB). Photos by R.L. Barrett.

The task of re-circumscribing the '*F. brachypoda* complex' begins here with segregation of the desert figs of Central Australia. Central Australian figs are recognisable as a single meta-population having long, narrow, almost hairless leaves, while the Pilbara and tropical populations of *F. brachypoda* show a multitude of variations. As well as obvious climatic difference between the tropical and desert populations of *F. brachypoda*, there appears to be a geographic gap of at least 150 km between the closest neighbouring desert and tropical collections. Though wind has been shown to transport pollinator wasps over 100 km, Nason *et al.* (1998) found most pollinators travel less than 14 km between individual figs.

Prior to the central Australia figs being grouped under *F. brachypoda*, they were commonly included in a loosely defined concept of *F. platypoda* A.Cunn. ex Miq. (Miquel 1847). The names *F. platypoda* var. *platypoda* (Miq.) Miq. and *F. platypoda* var. *minor* Miq. ex Benth. (1873) have both been applied to the desert figs. Dixon (2001a) noted that Corner considered *F. platypoda* var. *platypoda* from the inland of Northern Territory to be the most distinct form of *platypoda* and approached the appearance of *Ficus platypoda* var. *minor.*

The type specimens of *F. brachypoda* and *F. platypoda* both come from the Kimberley region of Western Australia, and the main concept of *Ficus platypoda* var. *minor* (sensu Bentham 1873) applies to plants from the Pilbara. There is currently no name available for the Central Australian desert fig, and as a newly defined species, it requires a new name.

The aims of this study were to:

1. Provide a diagnostic, morphological delimitation of the desert fig as a distinct species.
2. Test if a MaxEnt species range predication for the desert figs was restricted to central Australia or includes the Pilbara.
3. Test if morphological measurements from Dixon (2001a) could be used to successfully delimit the central Australian desert figs from all other figs in Dixon's data set.

Materials and Methods

Herbarium specimens have been examined at CANB, DNA, MEL, NSW and PERTH. Images of specimens (marked *) have been examined through JSTOR Plants (https://plants.jstor.org/; accessed July 2020), Kew Herbarium Catalogue (http://apps.kew.org/herbcat/gotoHomePage.do; accessed July 2020), Naturalis (https://bioportal.naturalis.nl/; accessed July 2020), and Muséum national d'Histoire naturelle (https://science.mnhn.fr/all/search; accessed July 2020).

Dixon's *Basal bract length* and *Internode length* were excluded because they lacked some data for both complexes. Where available, the latitude and longitude for each specimen was sourced from the *Atlas of Living Australia* (http://www.ala.org.au).

Specimen selection

Data for 25 morphological measurements of 133 figs from both Dixon's '*F. platypoda* complex' and '*F. leucotricha* complex' were acquired from Dixon (2001a). Study of voucher specimens used by Dixon (2001a) suggested that names had been applied to mixed taxonomic concepts, warranting reanalysis of morphological variation. For this study, Dixon's '*F. platypoda* complex' and '*F. leucotricha* complex' were combined into a single group. Any samples lacking latitude and longitude co-ordinates or missing data for any of the final variables were removed. Some records supplied by Dixon with 'PHD' numbers could not be found on ALA and were also excluded, while the locations for other 'PHD' numbers are given in Dixon's PhD thesis (Dixon 1999). This left 106 specimens from the original 133 in Dixon's study (see supplementary data) and included specimens variously identified as *F. atricha, F. brachypoda, F. cerasicarpa* and *F. platypoda*.

Variable Selection

Rather than attempting to delimit all taxa potentially present in Dixon's (2001a) study, we aimed to determine if central Australian populations formed a distinct group separate to Dixon's *F. platypoda* and *F. leucotricha* complexes. All of Dixon's variables were used except for Internode length (IL for '*F. platypoda*' group only) and Basal bract length (BBL for '*F. leucotricha*' group only), this left 22 variables (Table 2). Intercostal region sunken was added to the data set of Dixon (2001a).

Data Analysis

Original data from Dixon (2001a) contained 999 to show missing data, this was replaced with NA in the current study. Data analysis was performed using RStudio (RStudio Team 2015). Data was read in with the function read.csv with the na.strings option set to NA to prevent variable types being converted. Individuals with NA for any variable were removed with the na.omit function, this left a final set of 106 out of 133 specimens. A matrix containing the final variables was standardised with the scale command (centre true, scale true). Principle Component Analysis data was generated with the R function princomp and visualised as a scree plot to help decide on the most appropriate k value for the count of species clusters, in this case k = 4, which matched Dixon's conclusion that there were 4 species in the dataset.

In an attempt to recreate Dixon's results, data was explored with PCA and 2 clustering libraries 'pvclust' (Suzuki and Shimodaira 2006) and 'phangorn' (Schliep 2011); which contains a UPGMA function. All distance options were tested for pvclust (average, centroid, complete, mcquitty, median, single and ward.D) and UPGMA (average, complete, mcquitty, median and ward.D) to see which provided results that best matched Dixon's expected species clusters. Dendrogram results presented here were achieved by transposing the standardised data matrix to suit the pvclust command which was run with the Euclidean distance method, ward.D cluster method and nboot of 10,000 to create the AU (approximately unbiased) P values (%) for each node. Individual specimens from each cluster were then mapped with the R package Oz (Venables and Hornik 2016) and the points function.

Table 2. Data variables used in this study. All data except latitude and longitude (sourced from ALA 2020) are from Dixon (2001a). * marks the variables Dixon (2001a) found to most strongly separate *F. brachypoda* and *F. atricha.* Bolded variables were not used in the final analysis of this study. #Hair types: 0 = glabrous, 1 = clear, 2 = brown, 3 = clear and brown. Boolean 0 = false, 1 = true.

Variable	Abbreviation	Measurement Type
Specimen number		
Latitude decimal	Lat	decimal
Longitude decimal	Long	decimal
Leaf length	LL	mm
*Leaf width	LW	mm
Petiole length	PL	mm
Petiole width	PW	mm
Basal bract length (‘*F. leucotricha*’ only)	**BBL**	**mm**
Fig length	FL	mm
Fig diameter	FD	mm
Fig peduncle length	FPL	mm
Internode length (‘*F. platypoda*’ only)	**IL**	**mm**
Number of lateral veins	LV	count
Leaf shape	LS	decimal
Fig shape	FS	decimal
Basal vein angle	BVA	degrees
Lateral vein angle	LVA	degrees
Leaf apex	LA	degrees
Leaf base	LB	degrees
Basal bract pubescence	BBP	#0/1/2/3
*Fig pubescence	FP	#0/1/2/3
Peduncle pubescence	PP	#0/1/2/3
*Leaf pubescence adaxial surface	LPAD	#0/1/2/3
Leaf pubescence abaxial surface	LPAB	#0/1/2/3
*Leaf petiole pubescence	LPP	#0/1/2/3
*Stipule pubescence	SP	#0/1/2/3
*Young stem pubescence	SYP	#0/1/2/3
Intercostal region sunken	IR	boolean

Ecological Niche Modelling was performed in Maxent version 3.4.1 (Phillips *et al.* 2006; Phillips and Dudik 2008) via the spatial portal of Atlas of Living Australia (Atlas of Living Australia (http://www.ala.org.au). Accessed 30 December 2020). All *F. brachypoda* records were downloaded from Atlas of Living Australia (http://www.ala.org.au, Accessed 22 January 2020). A subset was created comprising specimens with “Coordinate Uncertainty in Metres” ≤ 100m. Specimens from the southern half of the Northern Territory regions of Alice Springs, Central Desert and MacDonnell Ranges along with the and north-west of South Australia were included in the model, with most records occurring in the Burt Plain, Central Ranges, Finke and Great Sandy Desert biogeographic regions (IBRA v7.0; Auricht 2014). Layers bio01 – bio19 (https://www.worldclim.org/data/bioclim.html) were selected to test each variable’s contribution to the maxent prediction. The top 5 contributing bioclim variables were then used to create the final maxent prediction. This included: Bio09 (el875) Temperature - driest quarter mean (35.8%), Bio04 (el892) Temperature - seasonality (15.3%), Bio07 (el862) - Temperature annual range (11.2%), Bio12 (el893) Precipitation - annual (9.4%), Bio17 (el889) Precipitation - driest quarter (6.9%). The prediction was created using 77 *F. brachypoda* collection records, 38 used for training, 4 for testing. 10038 background points and presence points were used to determine the Maxent distribution. Regularization values: linear/quadratic/product: 0.227, categorical: 0.250, threshold: 1.620, hinge: 0.500, Feature types used: hinge linear quadratic.

Results

For consistency with the study of Dixon (2001a), we discuss the two dendrograms presented in Fig. 4, where dendrogram A represents analysis of 22 variables and 106 individuals from Dixon (2001a) (dendrogram A); and data used to create dendrogram B includes an additional variable IR. Cluster 1 contains the same individuals in dendograms A and B. All 33 are from Dixon's *F. platypoda* group, including 30 that he identified as *F. atricha* and three as *F. brachypoda*. Cluster 2 contains the same seven individuals from Dixon's *F. leucotricha* group for both dendrograms, six that he identified as *F. platypoda* and one as *F. cerasicarpa*. Cluster 3 contains individuals from Dixon's *F. leucotricha* and *F. platypoda* groups for both dendrograms. For dendrogram A, cluster 3 contains 22 individuals including 16 from Dixon's *F. platypoda* group, all identified by Dixon as *F. brachypoda* and one which (though we determined one (*P03*) as the new species *F. desertorum*) and six individuals identified by Dixon as *F. cerasicarpa*. For dendrogram B, cluster 3 contains 32 individuals from Dixon's *F. leucotricha* and *F. platypoda* groups, 26 identified by Dixon as *F. brachypoda* and six identified as *F. cerasicarpa*. Cluster 4 for both dendograms contains individuals all from Dixon's *F. platypoda* group. In dendrogram A, cluster 4 contains 34 individuals identified by Dixon as *F. brachypoda,* 26 of which we determined as *F. desertorum*. In dendrogram B, cluster 4 contains 25 individuals, all from Dixon's *F. platypoda* group. Dixon identified all of these as *F. brachypoda,* but we determined all as *F. desertorum*. Samples in cluster 4 in dendrogram B are restricted to Central Australia, while clusters 1–3 for both dendograms are sympatric across northern and western Australia. Maxent Ecological Niche Modelling defines the highest probability envelope (>80%) for *F. desertorum* as localised to Central Australia (Fig. 6).

A pilot study using DArT sequencing, following the methods of Wilde *et al.* (2020), clearly separated multiple samples of *Ficus desertorum* from *F. brachypoda s.lat.* and a specimen of *F. atricha* (B.C. Wilde, unpubl. data).

Discussion

Using most of the morphological variables from Dixon (2001a) and an additional new variable (IR) we were able to separate a cluster (Fig. 4 B to cluster 4) of central Australian figs from other collections identified as *F. brachypoda*, *F. cerasicarpa* and *F. platypoda*. We note that sunken intercostal regions are diagnostic for the *F. brachypoda* complex as we define it (which remains highly variable even after the removal of *F. desertorum*), in contrast to the definition provided by Dixon (2001a) in his key and description. We consider a number of specimens included in *F. brachypoda s. lat.* by Dixon (2001a) to be better placed in *F. platypoda s. lat.*, so our concepts are not entirely equal, even in a broad sense of these species. The typical form of *F. brachypoda* has been examined in the field by RLB, along with images of the type collections, which each clearly show the sunken intercostal regions. The typical form is probably restricted to the north-west Kimberley region, but other forms with sunken intercostal regions still included in *F. brachypoda s. lat.* are very widespread from the southern Pilbara in Western Australia, north and east to central Queensland.

The other 3 clusters identified in Fig. 4 A and B may or may not represent valid groupings. No further analysis of these clusters was attempted, though there does appear to be some morphological order to these clusters that will be explored in future studies.

Within Cluster 1, most individuals identified by Dixon as *F. atricha* grouped together, though this study found no evidence for the absence of hairs as a delimiter for the species, with *F. brachypoda* sensu Dixon (2001a) also included within the cluster. Based on field observations by the authors, there is likely no single fig species spanning this distribution and this cluster probably represents multiple species. Cluster 2 contains all *F. platypoda* specimens and one individual of *F. cerasicarpa*. Dixon (2001a) considers these species to be allied and the cluster appears to make morphological sense with all individuals having large-leaves. Cluster 3 contains all the remaining *F. cerasicarpa* and some *F. brachypoda* specimens, with individuals spread over a wide range of WA, NT and western QLD. This cluster is unlikely to represent a single species. Individuals identified as *F. brachypoda* are found in three out of the four clusters, suggesting the species, as defined by Dixon (2001a), is not a natural taxon. No support was found for the separation of individuals into Dixon's '*F. leucotricha*' and '*F. platypoda*' complexes, with Cluster 3 including a combination of both complexes. Novel morphological measurements are likely to be required to delimit tropical Australian *Ficus* sect. *Malvanthera* species and there is likely no 'one size fits all' approach that will successfully delimit all species.

Though the results of these morphological analyses suggest that *F. desertorum* does not extend into the Pilbara region of Western Australia, plants from that region do appear very similar in leaf shape and petiole length, though differing in abaxial lamina venation (see Fig. 5). It is possible that the Pilbara meta-population is genetically isolated from the Central Australian plants by physical distance but it is considered more likely that it originated from an independent dispersal from northern Australia, and appears morphologically similar

due to convergent evolution as an adaptation to the arid environment. It is also possible that the Pilbara *F. brachypoda* populations have ongoing gene flow with disjunct fig populations along the Kimberley coastline of Western Australian.

The results of the current study are consistent with a molecular phylogenetic study by Bruun-Lund (2019). A specimen of *F. brachypoda* from central Australia (*Bruun-Lund 799*) included in his analysis did not resolved as sister to another *F. brachypoda* specimen from Litchfield National Park in tropical NT (*Bruun-Lund 791*), that instead grouped with two other tropical figs *F. cerasicarpa* and *F. subpuberula*. The central Australian *F. brachypoda* specimen (=*F. desertorum*) was strongly supported as a lineage sister to all three of these samples. A significant amount of work is still required to delimit species boundaries within the *F. brachypoda* species complex, including broad-scale collecting and sampling for genetic analyses.

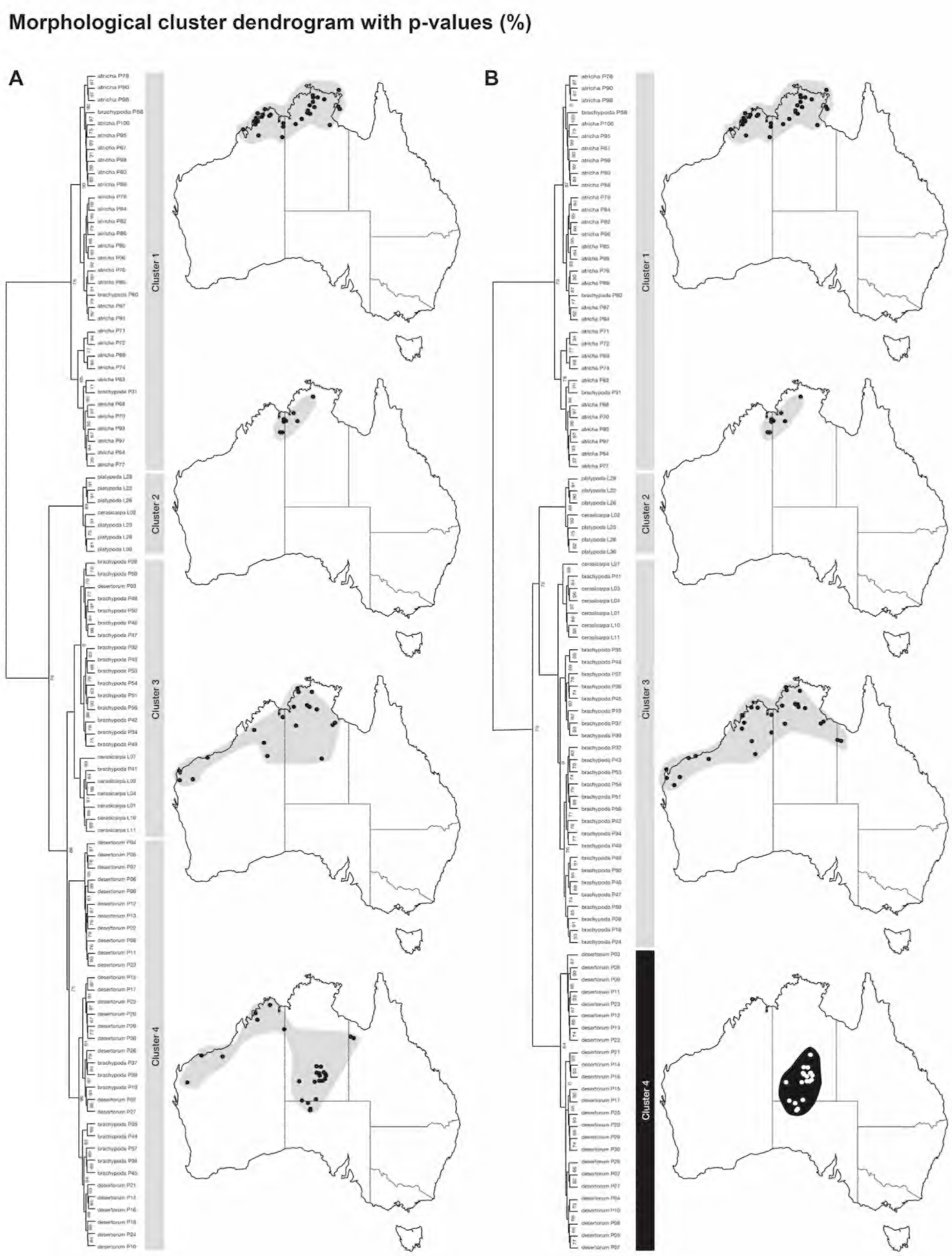

Fig. 4. Results of cluster analysis of the *Ficus brachypoda* and *F. platypoda* complexes based on morphological characteristics defined by Dixon (2001a). Dendrograms labelled with p-values on nodes and sample numbers from Dixon (2001a). Maps show distribution of individuals in each cluster. Dendrogram A with all of Dixon's morphological variables, Dendrogram B with an additional variable of sunken intercostal region.

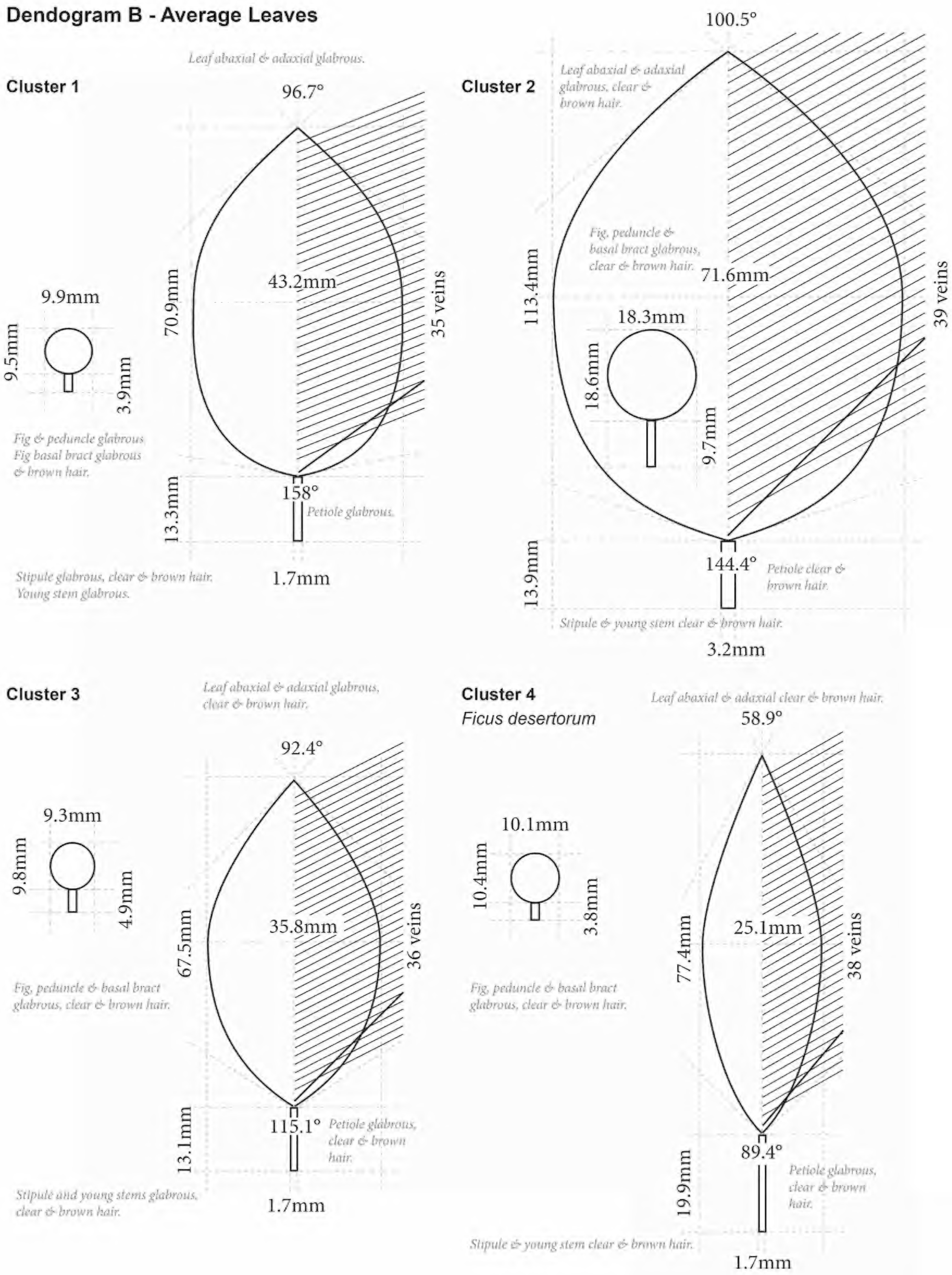

Fig. 5. Illustrations of the average leaf for each cluster of Dendrogram B representing the *Ficus brachypoda* and *F. platypoda* complexes using data from Dixon (2001a). Cluster 4 corresponds to *F. desertorum* as defined here.

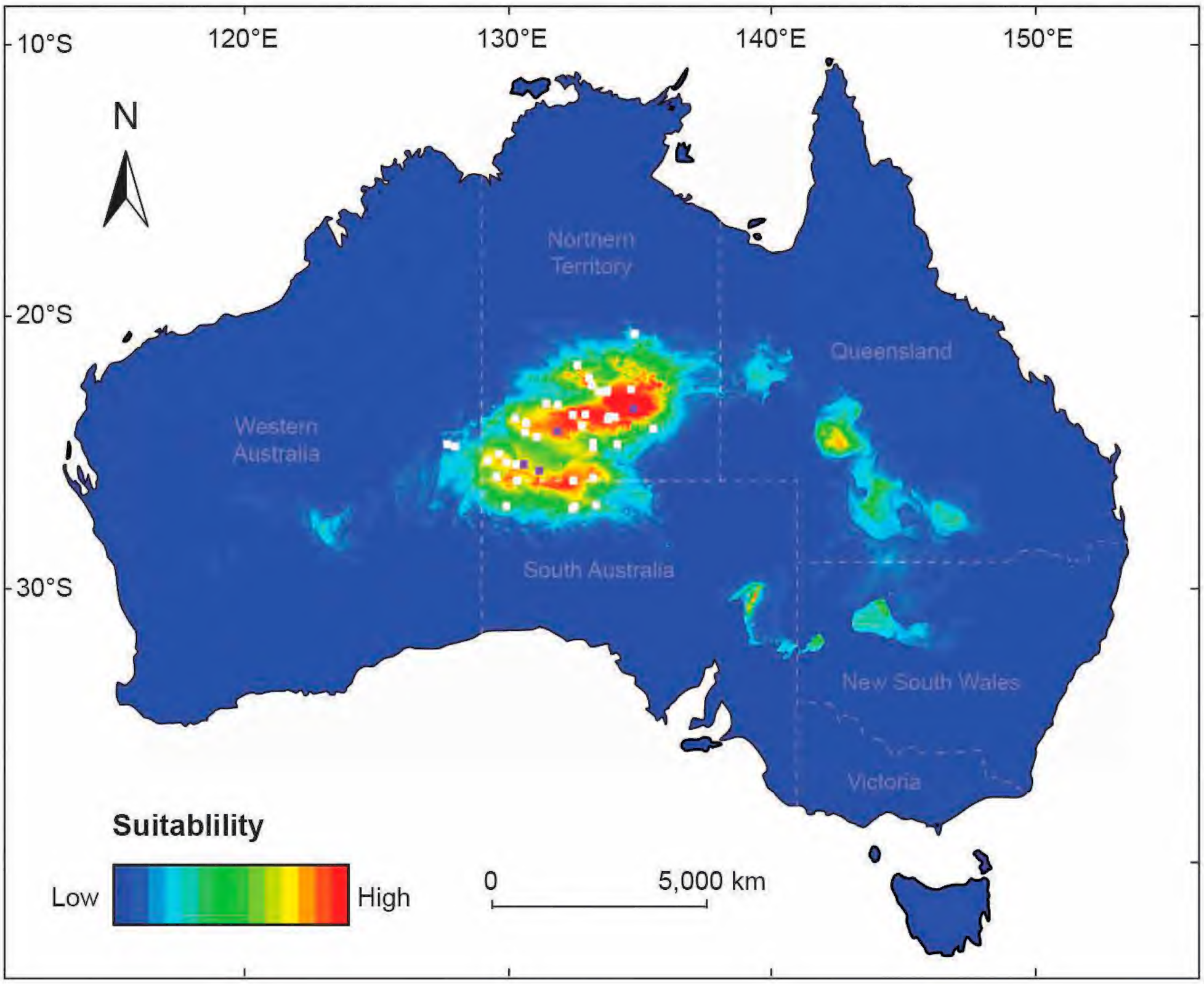

Fig. 6. Ecological Niche Modelling for *F. desertorum*. White dots represent the *F. brachypoda* occurrence records used to create the model, Violet dots are locations used by Maxent for testing (refer to Materials and Methods).

Taxonomy

While no name exists for the central Australian *Ficus* taxon at the rank of species, a single collection of this entity was included as a syntype of *Urostigma platypodum* forma *glabrior* by Miquel (1861) and the name *Ficus platypoda* var. *minor* (Bentham 1873) has also been applied with a similar circumscription. As no lectotypes have been previously designated for these names, we do so here to taxonomically exclude these names from our concept of *F. desertorum*.

Urostigma platypodum forma *glabrior* Miq., *J. Bot. Néerl.* 1: 236 (1861).

Type citation: '*Novae Hollandiae ora bor. occid.*: W. BYNOE, in *Herb. Hook., itineratores francogalli* in *Herb. Mus. Parisin.* – *Nova Holl. centralis* in tractu montium *M'Donnell*: STUART.'

Lectotype (here designated). 'Novae Holl. or. occ.' [Western Australia: N.W. coast, *B. Bynoe s.n.*] (lecto: K 001050896*; isolecto: U 0066831 [U.1424548]*, U 0066820 [U.1424547]*).

Residual syntype: 'Neu. holl. cot. occid., Voyage du Capitaine Baudin' (P 06762560*).

Excluded syntype (representing *Ficus desertorum*): Northern Territory: Brinkleys Bluff, MacDonnell Ranges, 1861, *J. McDouall Stuart s.n.* (syn: MEL 0239508, 239508!, U 0141619 [U.1424550]*).

Ficus platypoda var. *minor* Miq. ex Benth., *Fl. Austral.* 6: 169 (1873)

Type citation. 'N. Australia. N.W. Coast, *Bynoe*; Nicol Bay, *Gregory's* and *Ridley's* Expeditions.'

Lectotype (here designated). 'Novae Holl. or. occ.' [Western Australia: N.W. coast, *B. Bynoe s.n.*] (lecto: K 001050896*; isolecto: U 0066831 [U.1424548]*, U 0066820 [U.1424547]*).

Residual syntypes: Western Australia: Shark Bay, *F.T. Gregory s.n.* (syn: U 0142275*); Nicol Bay & De Grey River, 1863, *J.B. Ridley s.n.* (syn: K 001050895*).

Urostigma platypodum forma *minor glabrior* Miq. in Hooker, W.J., *London J. Bot.* 6: 562 (1847), *nom. illeg.*

Typification. We here select the *Bynoe* specimen at K as lectotype for both *Urostigma platypodum* forma *glabrior* Miq. and *Ficus platypoda* var. *minor* Miq. ex Benth. as it is a good fruiting specimen and it has Miquel's annotation as 'forma glabrior'. Bentham attributed his var. *minor* to Miquel, so it seems logical to choose a collection seen by both Bentham and Miquel as the lectotype of that name.

Notes. We currently include *Urostigma platypodum* forma *glabrior* and *Ficus platypoda* var. *minor* within a broadly defined *Ficus brachypoda*, with further research required to define taxon boundaries within this variable complex. We recommend not recognising this taxon at the rank of forma or variety.

Ficus desertorum B.C.Wilde & R.L.Barrett, **sp. nov.**

Type: Uluru (Ayers Rock-Mt Olga) National Park: Uluru (Ayers Rock), Mutitjulu (Maggie Springs) walk, on the ring road, 1.7 km NE of Ranger Station, 19 May 1988, *M. Lazarides & J. Palmer 252* (holo: CANB 385988; iso: DNA D0046821).

Illustrations: Laramba (Napperby) Community Women (2003; pl. p. 17, as *F. brachypoda*); Chew (1989; pl. 3, as *Ficus platypoda* var. *minor*); Jessop (1986; fig. 60, as *F. platypoda*); King (1986; fig. p. 41); Kutsche and Lay (2003; pls p. 85, as *F. brachypoda*); Latz (1995; fig. p. 196, pls p. 197, as *F. platypoda* var. *minor*); Low (1991; pl. p. 175, as *F. platypoda*); Moore (2005; pl. p. 192, as *F. brachypoda*); Urban (1990; pl., fig. p. 19); Womersley (1981; fig. 30, as *F. platypoda*).

Lithophytic multi-stemmed shrub, without buttresses; to around 4 m tall, branches spreading, 3–10 m wide; aerial roots usually absent, but sometimes rooting from decumbent branches. *Twigs* 2.0–6.5 mm diam. in fruit, ribbed when dry, often with a thin glaucous coating, puberulous with ascending hyaline hairs when young, soon glabrescent. *Leaves* alternate, loosely spirally arranged, often only persisting near branch tips and held erect to spreading. *Petiole* 9–34 mm long, 1.2–2.7 mm wide, flat to distinctly grooved above, commonly flattened below and ribbed when dry, finely puberulous with ascending hyaline hairs when young, soon glabrescent. *Lamina* coriaceous, (40–)46–120 mm long, (15–)19–44 mm wide; entire, lanceolate, occasionally broadly lanceolate or elliptic (widest point 30–50% along leaf blade from petiole); lateral veins (10–)12–18 pairs, looped at margin, 33.0–84.0°; basal veins sometimes indistinct, 24.0–119.0°, up to 1/10–1/6 the length of the lamina, tertiary venation reticulate to sub-scalariform; base acute to slightly obtuse, symmetric to slightly asymmetric; apex acute to obtuse; darker green when young (newest growth sometimes densely rusty-pubescent but usually white-pubescent if not glabrous), discolorous; *adaxial surface* glabrous or soon glabrescent, dark green, semi-glossy, not or lightly pruinose, midrib slightly raised, lateral veins flat to slightly sunken, sometimes indistinguishable, major and minor secondary veins similar in width, similar in colour to the blade, forming an indistinct reticulum, the surface appearing slightly spongy or blistered; cystoliths only on upper surface (hypergenous); *abaxial surface* glabrous or soon glabrescent, paler, mid-green to dark green, midrib flattened but distinctly raised, continuous with the petiole, yellow or cream, distinctly contrasting with the leaf lamina,; lateral veins ± flat or slightly raised. *Stipules* terminal, in pairs (10–)14–43(–62) mm long, lanceolate, caducous, sparsely puberulous with ascending hyaline hairs, glabrescent. *Basal bracts* 3, 2.2–6.2 mm long, free, imbricate, caducous, puberulous with ascending hyaline hairs. *Peduncle* (0–)1.5–9.7(–12.0) mm long, slender, 1.1–2.5 mm thick, ribbed when dry, pale green to green or yellow, sparsely to densely puberulous with ascending hyaline hairs. *Syconia* axillary, solitary or in pairs, 8.3–14.9 mm long, 7.8–16.3 mm diam.; obloid to spheroid, reddish brown when ripe, minutely pubescent at 40× magnification (appearing glabrous to the eye), punctate. *Ostiole* triradiate, prominent, 1.0–2.3 mm long, 2.2–4.8 mm wide, open, pubescent; *ostiolar bracts* 3, ovate, up to 1.0 mm long; internal ostiolar bracts ovate or deltoid, 0.8–1.0 mm long, glabrous; internal papillae abundant but minute; *interfloral bracts* ovate to lanceolate, 0.6–1.1 long, 0.3–0.5 mm wide, brown, glabrous, margins hyaline. *Female florets* embedded in wall of receptacle, sessile or pedicellate, 0.6–3.3 mm long; tepals 3 or 4; ovary ovoid or globose, 0.4–1.3 mm long; style 0.9–1.7 mm long, pale or whitish, glabrous; stigma bifid, papillose. *Male florets* very few, interspersed with the female and gall florets, ± sessile, *c.* 1 mm long; tepals 3 or 4, completely united, rarely free, spatulate, 0.8–1.2 mm long, reddish or whitish, glabrous; anther 1, *c.* 0.3 mm long, ovoid or oblong, dehiscence crescentic and longitudinal, filament *c.* 0.3 mm long. *Gall florets* sessile or pedicellate, 1.4–1.7 mm long, pedicel up to 0.4 mm long; tepals 3 or 4, free or united, ovate, *c.* 1.6 mm long, glabrous; ovary obovoid, 0.6–0.8 mm; style lateral, *c.* 0.3 mm long, glabrous; stigma simple. *Achenes* ovoid or sub-tetragonous, 0.8–1.5 mm in diam., surface ± smooth, very finely reticulate at 40× magnification. (Figs 7–9).

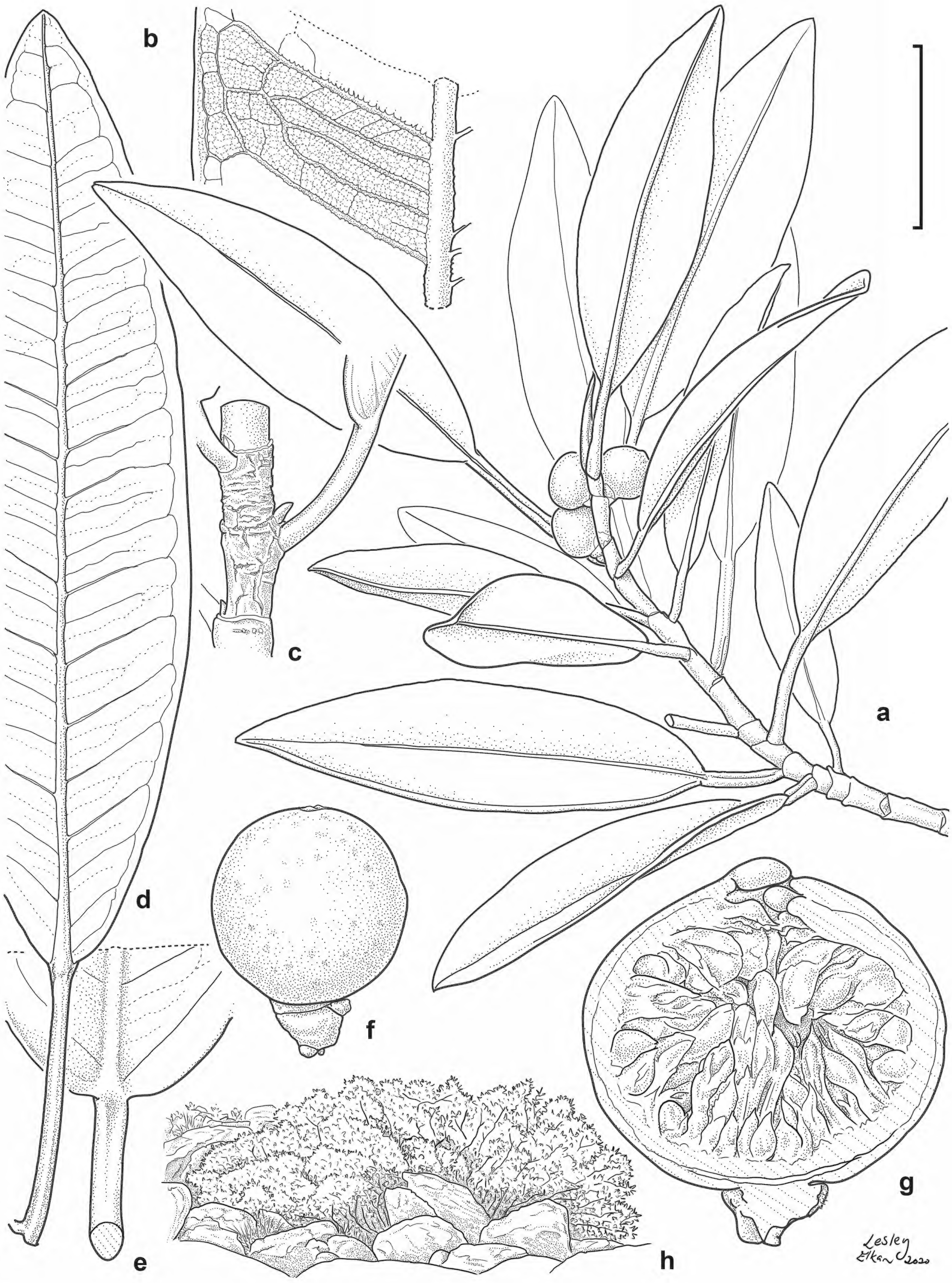

Fig. 7. *Ficus desertorum*. A: fruiting branch. B: detail of leaf venation, abaxial surface. C: detail of stem and petiole. D: leaf, abaxial surface. E: leaf base and petiole detail. F: mature fruit lateral view. G: longitudinal section of fruit. H: habit and habitat. Vouchers: A from *G. Chippendale s.n.* (NSW 927786); B, C, E-G from cultivated material; D from *G. Chippendale s.n.* (NSW 452252). Scale bar: A = 30 mm, b = 10 mm, c, e, f = 15 mm, d = 20 mm, g = 5 mm, h = no scale. Illustration by Lesley Elkan.

Fig. 8. *Ficus desertorum*. A: habit on Uluru, NT. This individual has a decumbent habit and flows down the face of Uluru. B, C: foliage and young figs showing typical upright branches and leaves, Karlu Karlu, NT. D: variation in leaf shape. This individual is growing in sand, Simpsons Gap, NT. E: Fruiting branchlet on cultivated plant. F: Figs, petioles and apical bracts on cultivated plant. Photos: A–D by B.C. Wilde; E, F by R.L. Barrett.

Diagnostic characters. Distinguished from other Australian species in *Ficus* section *Malvanthera* by having stiff lanceolate, dark green, discolorous leaves; many parallel, often obscure lateral veins; petioles that are continuous with the midrib (not constricted); leaves with minute, white or rusty hairs and not or slightly sunken intercostal regions on the lower surface (the aeroles appearing very slightly raised). The leaves of this species separate it from most other native Australian figs, with petioles 9–34 mm long, 1.2–2.7 mm wide, and the lamina lanceolate (occasionally broadly lanceolate or elliptic), (40–)46–120 mm long, (15–)19–44 mm wide, a distinctive length/width ratio (Fig. 5). Some populations of *F. brachypoda s. lat.* from the Pilbara region of Western Australia do have a similar leaf shape, but all specimens assigned to *F. brachypoda s. lat.* differ in the strongly sunken, finely reticulate intercostal regions (or intercostal veins appearing raised) on the lower surface.

Fig. 9. *Ficus desertorum*. A: abaxial leaf surface. B: abaxial leaf surface at junction with petiole. C: close-up of smooth adaxial leaf surface. D: close-up of abaxial leaf surface with flat or scarcely sunken intercostal regions (pale areas surrounded by reticulate veins). E, F: fruit. Photos by R.L. Barrett from a cultivated plant.

Selected specimens examined: (30 of c. 450): WESTERN AUSTRALIA: Blackstone Ranges, 2 Aug. 1967, *R.C. Carolin 6032* (AD, *n.v.*, L*); Mount Eveline, E of Warburton Mission, 27 Aug. 1961, *A.S. George 2924* (PERTH); Pangkupirri Rockhole, Walter James Range, 22 Sept. 2006, *H.P. Vonow, V.T. Clarke, W.A. Thompson HPV 3073* (AD, PERTH); Rawlinson Range, 400 m W of Yirrima Springs, 46 km NW of Giles Meteorological Station, 17 Aug. 2012, *N.G. Walsh 7613* (MEL, PERTH). NORTHERN TERRITORY: Devils Marbles, *c.* 63 miles [101.3 km] S of Tennant Creek, 16 June 1967, *B.G. Briggs 1205* (NSW); 53 km E by N [from] Alice Springs, 6 Oct. 1978, *J.C. Cardale s.n.* (CANB 278054); 32 km WNW Alice Springs, 8 Oct. 1978, *J.C. Cardale s.n.* (CANB 278053); Palm Valley National Park, Palm Creek, 25 June 1974, *G.W. Carr 2095* (DNA, MEL, NSW); Alice Springs, 25 Nov. 1954, *G.M. Chippendale 683* (DNA, NSW); Jessie Gap, MacDonnell Ranges, 30 May 1997, *L.A. Craven, C.L. Brubaker & J. Grace 9652* (CANB); 800 m by road from Ormiston Gorge campground towards Namatjira Drive, West MacDonnell Ranges, 21 Sept. 2018, *M.D. Crisp 11793* (CANB); Alice Springs, May 1939, *Mrs Dale s.n.* (NSW 452254); Ross Highway, E of Alice Springs, Mt Benstead creek crossing, 21 Oct. 1997, *D. Dixon & I. Champion PHD484* (CANB, DNA, JCT); MacDonnell Ranges, 23 Mar. 1911, *G.F. Hill 121* (MEL); Finke River, 1880, *F.A.H. Kempe 211* (MEL); 45 km W of TiTree Roadhouse, 22 July 1992, *P.K. Latz 12370* (CANB, DNA, NT); 10 miles NE of Woodgreen Station, 23 May 1955, *M. Lazarides 5278* (AD, CANB,

MEL, NSW); Tephrina Gorge, 10 Feb. 1985, *G.J. Leach 520* (CANB, DNA, K, MEL, NSW, UPNG); Yalkipi / Alkipi, *c.* 11.4 km due SW of Papunya, 21 Jan. 1984, *D. Nash 25* (CANB); Umbeara (Alice Springs District), Nov. 1965, *J.C. Newman s.n.* (CANB 00829250); 15 miles NE of Yambah Station, 10 Mar. 1953, *R.A. Perry 3381* (CANB); Prowse Gap, Stuart Hwy, 12 April 1979, *M.O. Rankin* 1912 (AD, DNA, MEL, PERTH); by SE base of Ayers Rock which is c. 350 km SW of Alice Springs, 31 Aug. 1957, *R. Schodde 419* (AD, CANB); Vaughan Springs, 4 July 1954, *R.E. Winkworth 422* (CANB). SOUTH AUSTRALIA: Cheesman Peak, N face, below and to the W of the summit, 28 Aug. 1978, *W.R. Barker 2927* (AD, MEL); Everard Ranges, Everard Park. Betty Well area, 25 June 1965, *A.C. Beauglehole 10186* (AD, MEL, NSW); NW of Watarru Rock; *c.* 5 km E of Watarru Community, 15 July 2000, *A. Christie 80* (AD, CANB, DNA, NT); 20 miles W of Tieyon Homestead, *P.L. Milthorpe s.n.* (CANB 831889); Mount Lindsay, 6 Aug. 1962, *D.E. Symon 2578* (AD, PERTH); between Betty and Ronalds Well, Everard Park Station, Everard Ranges, Feb. 1965, *D.E. Symon 3346* (AAU, AD, CANB, K).

Distribution. Most common in the greater MacDonnell Ranges of the Northern Territory, from the Devils Marbles, south to the Everard Ranges in South Australia and west to the Rawlinson and Walter James Ranges in Western Australia (Fig. 2A, within dashed ellipse).

Ecology. Usually on rocky sandstone, quartzite, or siliceous slopes, ridges and cliff faces, or on large granite or sandstone boulder fields, often associated with drainage lines, water-accumulation points and waterholes, the roots commonly following rock fissures. While mostly growing in rock fissures with little or no soil, it has occasionally been recorded growing in alluvial sand or in rocky red soil adjacent to rocky outcrops. Commonly growing in isolation on rock faces with few directly associated species, but recorded in association with *Acacia aneura*, *A. kempeana*, *A. olgana*, *A. tetragonophylla*, *A. victoriae*, *Atalaya hemiglauca*, *Callitris glaucophylla*, *Cheilanthes sieberi*, *Corymbia opaca*, *Cymbopogon ambiguus*, *Cyperus cunninghamii*, *C. iria*, *Dodonaea viscosa*, *Eragrostis sterilis*, *Eriachne mucronata*, *Eucalyptus camaldulensis*, *Laurentia* (*Isotoma*) *petraea*, *Livistona mariae*, *Macrozamia macdonnellii*, *Ptilotus obovatus*, *P. polystachyus*, *Santalum lanceolatum*, *Senna* spp., *Themeda triandra*, *Triodia irritans*, *Tripogonella loliiformis*, and the introduced grass *Cenchrus ciliaris*.

Phenology. Flowering and fruiting all year round following rainfall, but the main fruiting time appears to be August to January.

Conservation status. The species is widespread and present in a number of national parks and other conservation reserves, but it is usually only found as small populations, so threats such as fire may have localised impacts.

Etymology. The epithet refers to the unusual habitat of this species (for *Ficus*) in the arid centre of Australia, dominated by desert environments.

Indigenous names. *tywerrk* (Alyawarr; Anmatyerr); *tjurrka* (Arrente); *utyeerk*, *utyeerke* (Eastern Arrente); *tywerrke* (Western Arrente); *iḻi*, *witjirrki*, *yiḻi* (Pintupi); *iḻi* (Pitjantjatjara / Yankunytjatjara); *wÿirrki* (Warlpiri). The figs as a food are known as *mai puḻka* (Yankunytjatjara). (See Kemp 1891; Cleland and Johnston 1933, 1937, 1939; Johnstone and Cleland 1943; Meggitt 1957; Cleland and Tindale 1959; Maconochie 1970; Hale 1975; Hansen and Hansen 1977; O'Connell *et al.* 1983; Latz 1995; Everard *et al.* 2002.)

Common names. Desert fig (preferred); Wild fig; Rock fig; Native fig.

Ethnobotany. Desert figs are an important traditional food source for many Aboriginal people in Central Australia, being rich in both calcium and potassium (Low 1991). Only ripe figs are picked by Anmatyerr people, immature figs being left to mature (Laramba (Napperby) Community Women 2003). Around Mount Liebig, the desert fig fruit grow in summer and are eaten when yellow and still raw (Nash 1984). Desert fig has the advantage of providing tens of thousands of fruit (each c. 2.5 g fresh, 1 g dry) from a single tree, and early European settlers even used the fruit to make jam (O'Connell *et al.* 1983; Latz 1995). Fruit not eaten when ripe (by people, birds or wallabies), fall to the ground and dry hard and intact, providing a long-lasting food source that can be ground up with water and / or wild honey (Latz 1995; Moore 2005). Dry figs that are ground with water can be formed into balls that can then be re-dried and stored for long periods for consumption when other foods are scarce (Latz 1995). Dried figs were traditionally gathered during the winter months of June to August in some areas north of Alice Springs (Tindale 1981; Specht and Specht 1999). This species was traditionally a critical food source during dry periods due to the abundance of fruit, and habitat around waterholes which are critical environments during periods of drought (Latz 1995). An increase ceremony, intended to maximise fruit production, is described by Mountford (1950) and the fact that a ceremony has been dedicated to fruit production in this species indicates its cultural significance.

In addition to utilisation for food, the leaves of this species were used for children's games, women's leaf games, and love potions (Latz 1995).

The desert fig features prominently in local oral histories and is a totemic species for the eastern Pitjantjatjara people, of sufficient importance that damaging a plant could result in a death penalty (Tindale 1941; Womersley 1981; Low 1991; Latz 1995). In more recent times, seedlings and cuttings have been transplanted to local communities as an ongoing source of traditional food (Nash 1993). Seedlings were also historically transplanted to important waterholes as a source of food (Nash 1993), so at least some of the present populations are likely due to human-mediated dispersal.

Notes. Latz (1995) records that roots form on lateral branches in good seasons, and main roots can extend up to 50 m down cliff faces, following rock fissures to moisture. Sensitivity to both fire and frost is noted by Latz (1995). Around Lake McKay, fires would not be lit near culturally valuable fig trees to protect the valuable fruit (Edwards and Allan 2009).

Plants cultivated in Sydney stay true to type and form ripe fruit, possibly pollinated by wasps that normally pollinate *F. obliqua* G.Forst. Hybrid seedlings from cultivated plants have been grown for >5 years and most are healthy and strong. They appear morphologically intermediate between *F. desertorum* and *F. obliqua*. Plants of *F. obliqua* and *F. desertorum* cultivated together set fruit at the same time.

The fruit of *F. desertorum* is eaten by the Western bowerbird *Ptilonorhynchus guttatus guttatus* (Gould) (Fig. 10). The distribution of this bowerbird subspecies is very similar to that of the desert figs in Central Australia and it has a strong (though not exclusive) ecological link to the fig trees as fruit are available all year round, the fig trees often grow near water, and the dense cover offers excellent sites for bower construction (Frith and Frith 2008). This somewhat mutualistic association was documented by Eylmann (1911), with more detailed observations provided by McGilp (1931). A summary of known observations is provided by Higgins *et al.* (2006). The Western bowerbird might be the vector of desert figs growing on inaccessible cliffs and located many kilometres away from their nearest neighbours through consumption of fruit.

While most specimens here included in *Ficus desertorum* were determined as *F. brachypoda* by D.J. Dixon, some specimens were determined as a range of other *Ficus* species.

Fig. 10. Western Bowerbird with the foliage of *Ficus desertorum* in the background and fruit in its beak. Photo by Tim Rudman (CC BY-NC-ND 3.0).

Acknowledgements

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References

Atlas of Living Australia (2020) The Australasian Virtual Herbarium. https://avh.chah.org.au/ (Accessed 16 June 2020)

Auricht CM (2014) Interim Biogeographic Regionalisation for Australia (IBRA), Version 7 (Regions). https://www.environment.gov.au/land/nrs/science/ibra (Accessed 27 May 2021) https://doi.org/10.13140/2.1.1858.3840

Bentham G (1873) *Flora Australiensis: a description of the plants of the Australian territory. Vol. VI. Thymeleæ to Dioscorideæ*. (L. Reeve and Co., London) https://doi.org/10.5962/bhl.title.141

Berg CC, Corner EJH (2005) Moraceae (*Ficus*). In *Flora Malesiana: Series 1. Seed plants. Vol. 17, part 2.* (Nationaal Herbarium Nederland: Leiden, Netherlands)

Brand-Miller JC, Holt SHA (1998) Australian Aboriginal plant foods: a consideration of their nutritional composition and health implications. *Nutrition Research Reviews* 11: 5–23. https://doi.org/10.1079/NRR19980003

Bruun-Lund S (2019) *Darwin's abominable mystery – and evolution and diversification of* Ficus *L.* PhD thesis, University of Copenhagen. http://www2.bio.ku.dk/bibliotek/phd/Sam%20Bruun-Lund.pdf

Chew W-L (1989) Moraceae. In: AS George (Ed.) *Flora of Australia. Volume 3: Hamamelidales to Casuarinales*. pp. 15–68. (Australian Government Publishing Service: Canberra)

Clarke PA (2007) *Aboriginal people and their plants*. (Rosenberg Publishing: Dural, NSW)

Clarke PA (2008) *Aboriginal plant collectors. Botanists and Australian Aboriginal people in the Nineteenth Century*. (Rosenberg Publishing: Dural, NSW)

Clarke PA (2012) *Australian plants as Aboriginal tools*. (Rosenberg Publishing: Dural, NSW)

Cleland JB (1932) Botanical notes of anthropological interest, from MacDonald Downs, Central Australia. *Transactions and Proceedings of the Royal Society of South Australia* 56: 36–38. https://www.biodiversitylibrary.org/item/129826#page/46/mode/1up

Cleland JB, Johnston TH (1933) The ecology of the Aboriginies of Central Australia. *Transactions and Proceedings of the Royal Society of South Australia* 57: 113–124. https://www.biodiversitylibrary.org/item/129836#page/134/mode/1up

Cleland JB, Johnston TH (1937) Notes on native names and uses of plants in the Musgrave Ranges region. *Oceania* 8: 208–215. https://doi.org/10.1002/j.1834-4461.1937.tb00416.x

Cleland JB, Johnston TH (1939) Aboriginal names and uses of plants at the Granites, Central Australia. *Transactions of the Royal Society of South Australia* 63: 22–26. https://www.biodiversitylibrary.org/item/129823#page/29/mode/1up

Cleland JB, Tindale NB (1954) Ecological surroundings of the Ngalia natives of Central Australia and the native names and uses of plants. *Transactions and Proceedings of the Royal Society of South Australia* 77: 81–86. https://www.biodiversitylibrary.org/item/128922#page/103/mode/1up

Cleland JB, Tindale NB (1959) The native names and uses of plants at Haasts Bluff, Central Australia. *Transactions and Proceedings of the Royal Society of South Australia* 82: 123–140. https://www.biodiversitylibrary.org/item/127470#page/141/mode/1up

Corner EJH (1960) Taxonomic notes on *Ficus* Linn., Asia and Australasia I. Subgen. *Urostigma* (Gasp.) Miq. *The Gardens' Bulletin Singapore* 17: 368–485. https://www.biodiversitylibrary.org/item/148092#page/408/mode/1up

Corner EJH (1965) Check-list of *Ficus* in Asia and Australasia with keys to identification. *Gardens Bulletin, Singapore* 21: 1–162. https://www.biodiversitylibrary.org/item/148078#page/13/mode/1up

Dixon DJ (1999) *Figuring out the figs: systematic studies in Ficus (Urostigma sect. Malvanthera)*. PhD Thesis, James Cook University. https://researchonline.jcu.edu.au/33767/1/33767-dixon-1999-thesis.pdf

Dixon DJ (2001a) A chequered history: the taxonomy of *Ficus platypoda* and *F. leucotricha* (Moraceae: *Urostigma* sect. *Malvanthera*) unravelled. *Australian Systematic Botany* 14: 535–563. https://doi.org/10.1071/SB00028

Dixon DJ (2001b) *Ficus lilliputiana* (Moraceae), a new species from the Kimberley region of Western Australia and the Northern Territory. *Nuytsia* 13: 457–464. https://florabase.dpaw.wa.gov.au/nuytsia/article/348

Dixon DJ (2002) A comparison of the leaf anatomy of *Ficus subpuberula*, *F. atricha* and *F. brachypoda* (Moraceae). *Nuytsia* 15: 27–32. https://florabase.dpaw.wa.gov.au/science/nuytsia/385.pdf

Dixon DJ (2003) A taxonomic revision of the Australian *Ficus* species in the section *Malvanthera* (*Ficus* subg. *Urostigma*: Moraceae). *Telopea* 10: 125–153. https://doi.org/10.7751/telopea20035611

Dixon DJ, Jackes BR, Bielig LM (2001) Figuring out the figs: the *Ficus obliqua–Ficus rubiginosa* complex (Moraceae: *Urostigma* sect. *Malvanthera*). *Australian Systematic Botany* 14: 133–154. https://doi.org/10.1071/SB99029

Edwards GP, Allan GE (Eds) (2009) *Desert fire: fire and regional land management in the arid landscapes of Australia*. DKCRC Report 37. (Desert Knowledge Cooperative Research Centre, Alice Springs) http://www.nintione.com.au/resource/DKCRC-Report-37-Desert-Fire_fire-and-regional-land-management-in-the-arid-landscapes-of-Australia.pdf

Eylmann E (1911) Die vogelwelt der kolonie Südaustralien. *Journal für Ornithologie* 59 (Suppl. 2): 93–148. https://www.biodiversitylibrary.org/item/43503

Everard P, Everard M, Murika, Tjampu T, Kanytji, Pumani S, Milatjari, Goddard C, Kalotas A (2002) *Punu: Yankunytjatjara plant use. Traditional methods of preparing foods, medicines, utensils and weapons from native plants*. Revised edn. (Jukurrpa Books: Alice Springs)

Frith CB, Frith DW (2008) *Bowerbirds: nature, art and history*. (Frith & Frith: Malanda, Qld)

Hale KL (1975) *Walpiri to English vocabulary*. (Institute for Aboriginal Development: Alice Springs)

Hansen KC, Hansen LE (1977) *Pintipi/Luritja to English dictionary*. (Institute for Aboriginal Development: Alice Springs)

Henderson RJF (1993) The correct names for two Australian varieties of *Ficus* L. (Moraceae). *Austrobaileya* 4: 119–120. https://www.jstor.org/stable/41738838

Higgins PJ, Peter JM, Cowling SJ (Eds) (2006) *Handbook of Australian, New Zealand & Antarctic Birds. Volume 7 Part A Boatbills to Starlings*. (Oxford University Press: South Melbourne)

Jessop JP (1986) Moraceae. In JP Jessop and HR Toelken (Eds) *Flora of South Australia. I. Lycopodiaceae-Rosaceae. Handbook of the flora and fauna of South Australia*. 4th edn. pp. 116 (South Australian Government Printing Division: Adelaide)

Johnstone TH, Cleland JB (1943) Native names and uses of plant in the north-eastern corner of South Australia. *Transactions and Proceedings of the Royal Society of South Australia* 67: 149–173. https://www.biodiversitylibrary.org/item/129832#page/171/mode/1up

Kemp H (1891) A grammar and vocabulary of the language spoken by the Aborigines of the MacDonald Ranges, Central Australia. *Transactions and Proceedings of the Royal Society of South Australia* 14: 1–54. https://www.biodiversitylibrary.org/item/84660#page/9/mode/1up

King P (Ed.) (1986) *Plant identikit: common plants of Central Australia*. (Conservation Commission Northern Territory: Darwin)

Kirk R (1996). Practical significance: a concept whose time has come. *Educational and Psychological Measurement* 56: 746–759. https://doi.org/10.1177/0013164496056005002

Kutsche F, Lay B (2003) *Field guide to the plants of outback South Australia*. (Department of Water, Land and Biodiversity Conservation: Adelaide)

Laramba (Napperby) Community Women, Green JA (2003) *Anmatyerr Ayey Arnang-akert. Anmatyerr plant stories*. (IAD Press: Alice Springs)

Latz PK (1995) *Bushfires and bushtucker. Aboriginal plant use in Central Australia*. (IAD Press: Alice Springs, NT)

Latz PK (2007) *The flaming desert. Arid Australia – a fire shaped landscape*. (Peter Latz: Alice Springs)

Latz PK, Griffin GF (1978) Changes in Aboriginal land management in relation to fire and to food plants in central Australia. Pp. 77–85 in BS Hetzel and HJ Frith (Eds) *The nutrition of Aboriginies in relation to the ecosystem of Central Australia*. (CSIRO: Melbourne)

Low T (1991) *Wild food plants of Australia*. (Angus & Robertson: Pymble, NSW)

Maconochie JR (1970) Pitjantjatjara names of some Central Australian plants. *The South Australian Naturalist* 44: 75–77.

McGilp JN (1931) Observations on the Western Bower-Bird (*Chlamydera guttata*). *South Australian Ornithologist* 11: 98–101. https://birdssa.asn.au/images/saopdfs/Volume11/1931V11P098.pdf

Meggitt MJ (1957) Notes on the vegetable foods of the Walbiri of Central Australia. *Oceania* 28: 143–145. https://doi.org/10.1002/j.1834-4461.1957.tb00734.x

Miquel FAW (1847) Prodromus Monographiae Ficuum. *London Journal of Botany* 6: 514–588. https://www.biodiversitylibrary.org/item/6317#page/556/mode/1up

Miquel FAW (1861) Note sur les figuiers de la Nouvelle-Hollande. *Journal de Botanique Néerlandaise* 1: 230–243.

Miquel FAW (1867–8) Annotationes de *Ficus* speciebus. *Annales Musei Botanici Lugduno-Batavi* 3: 260–288. https://www.biodiversitylibrary.org/item/2545#page/289/mode/1up

Mountford CP (1950) *Brown men and red sand: Journeyings in wild Australia*. (Angus and Robertson: Sydney)

Mountford CP (1962) *Ayers Rock: its people, their beliefs and their art*. (Angus & Robertson: Sydney)
Moore P (2005) *A guide to plants of inland Australia*. (Reed New Holland: Sydney)
Nash D (1984) *An ethnobotanical study of women's plant use at Mt Leibig*. Honours Thesis. Australian National University: Canberra.
Nash D (1993) *Aboriginal gardening: plant resource management in three Central Australian communities*. Masters Thesis. The Australian National University: Canberra.
Nason JD, Herre EA, Hamrick JL (1998) The breeding structure of a tropical keystone plant resource. *Nature* 391: 685–687. https://doi.org/10.1038/35607
O'Connell JF, Latz PK, Barnett P (1983) Traditional and modern plant use among the Alyawarra of Central Australia. *Economic Botany* 37: 80–109. https://doi.org/10.1007/BF02859310
Phillips S, Anderson R, Schapire R (2006) Maximum entropy modelling of species geographic distributions. *Ecological Modelling* 190: 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026
Phillips SJ, Dudik, M (2008) Modelling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31: 161–175.
RStudio Team (2015). *RStudio: Integrated Development for R*. RStudio, Inc., Boston, MA. http://www.rstudio.com/
Schliep K, (2011) phangorn: phylogenetic analysis in R. Bioinformatics. *Bioinformatics* 27(4):592-593. https://doi:10.1093/bioinformatics/btq706
Specht RL, Specht A (1999) *Australian plant communities: dynamics of structure, growth and biodiversity*. (Oxford University Press: Melbourne)
Suzuki R, Shimodaira H (2006) Pvclust: an R package for assessing the uncertainty in hierarchical clustering. *Bioinformatics* 22: 1540–1542. https://doi.org/10.1093/bioinformatics/btl117
Sweeney G (1947) Food supplies of a desert tribe. *Oceania* 17: 289–299. https://doi.org/10.1002/j.1834-4461.1947.tb00154.x
Tindale NB (1941) A list of plants collected in the Musgrave and Mann Ranges, South Australia, 1933. *The South Australian Naturalist* 21: 8–12. https://www.biodiversitylibrary.org/item/132610#page/10/mode/1up
Tindale NB (1981) Desert Aborigines and the southern coastal peoples: some comparisons. In: A Keast (Ed.), *Ecological biogeography of Australia*. pp. 1855–1884. (The Hague: Junk)
Urban A (1990) *Wildflowers and plants of inland Australia*. (Southbank Editions: Port Melbourne)
Venables B, Hornik K (2016) oz: Plot the Australian Coastline and States. R package version 1.0-21. https://CRAN.R-project.org/package=oz
Wilde BC, Rutherford S, van der Merwe M, Murray ML, Rossetto M (2020) First example of hybridisation between two Australian figs (Moraceae). *Australian Systematic Botany* 33: 436–445 https://doi.org/10.1071/SB19048
Wilson D, Wilson A (2013) Figs as a global spiritual and material resource for humans. *Human Ecology* 41: 459–464. https://doi.org/10.1007/s10745-013-9582-z
Womersley JS (1981) Moraceae. In JP Jessop (Ed.) *Flora of Central Australia*. pp. 16–17. (Australian Systematic Botany Society / A.H. & A.W. Reed Pty Ltd: Sydney)

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Grevillea trichantha Olde, a third species with hairy flowers in the *Triloba* Group (Proteaceae: Grevilleoideae: Hakeinae) from the Marchagee Track, south-west Western Australia

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Abstract

Grevillea trichantha Olde, a rare species in the *Triloba* Group is described. It appears to be most closely related to another rare species, *G. metamorpha* Makinson and is more common, though its localised distribution still requires a high conservation priority. *Grevillea trichantha* is the third species in the *Triloba* Group in which the perianth is consistently, but not always uniformly, hairy. A short key differentiating the three species is provided.

Introduction

This paper is the fourth in a series aimed at resolving the taxonomy of the *Triloba* Group of *Grevillea sensu* Makinson (2000); see Olde 2020, 2021; Olde and Marriott 2021). Only two hairy-flowered species have been distinguished to date in the *Triloba* Group and to these a third, *G. trichantha,* is here added. *Grevillea erinacea* Meisn. was the first species to be described (Meisner 1855: 74). It was gathered during James Drummond's sixth and last collection to the north of Perth. Makinson (2000: 506) described the second species, *Grevillea metamorpha,* which was brought to attention by staff of the Western Australian Herbarium. This species seems to have the greatest affinity with *G. trichantha*, notwithstanding that none of the species have been phylogenetically tested using molecular data. *Grevillea metamorpha* is the rarest of the three, known only from a single, seed-obligate population in a degraded habitat on private land in the Warradarge district to the north-west of the population of *G. trichantha.* All three species have smooth fruits. Hairs on the floral parts, particularly the outer surface of the perianth, of these three species were often observed to be variable in density and, rarely altogether absent, or quickly caducous.

The distribution of hairs on the inflorescence, floral and vegetative parts reliably discriminates species in the *Triloba* Group. However, as McGillivray and Makinson (1993: 167) have pointed out, 'developmental abnormalities in flowers were more evident in this group than in other groups'. Pollen abnormalities in *G. vestita*, were first noted by Venkata Rao (1964). Venkata Rao (1966: 174) also observed free staminal filaments in some flowers of that species (normally adnate to the tepals). McGillivray and Makinson (1993) reported tepals 5 or more per flower (normally four), deformed styles, digynous and misshapen pollen (normally triporate). Makinson noted two pistils emergent from a single pedicel on a specimen sheet at CANB. In this examination of the Group the presence of random hairs on various floral organs that do not normally possess them was noted along with fusion of pedicels or styles and digynous styles.

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The discussion on morphological and developmental abnormalities is relevant to a unique situation in the conceptual definition of *Grevillea trichantha*. Within the distribution of its population which extends over c. 1 km and involves numerous plants and ramets, all with hairy perianths, a single plant (*Olde* 01/46) was observed with glabrous flowers, leading initially to the belief that two species may have been present at the site. Microscopic comparison showed that it was otherwise indistinguishable from *G. trichantha,* apart from some simple hairs at the base on the adaxial surface of the perianth. Morphological conflicts exclude its inclusion in any another glabrous-flowered species such as *G. acrobotrya* Meisn., a seed-obligate species with a fusiform pollen-presenter and chocolate perianth limb, *G. amplexans* Diels, another seed-obligate species with amplexicaul leaves, *G. uniformis* (McGill.) Olde which has truncated leaf bases and *G. vestita* (Endl.) Meisn. which has a spreading vegetative indumentum. Since it lacked a population base, it was taken as a genetic variant or possible hybrid, the parentage of which could not be inferred from co-occurring plants.

The basis for any taxonomic decisions must be morphological consistency at the population level. However, the presence of occasional aberrant specimens does not invalidate a species concept and can simply be part of the evolutionary process. Along with the high reported and observed incidence of morphological abnormality in the *Triloba* Group, it was decided here to treat the glabrous-flowered specimen of *G. trichantha* (*Olde* 01/46) as 'abnormal' by virtue of the random and infrequent absence of floral hairs in the population as a whole. The species has therefore been conceptualised in terms of the morphology of the majority of individuals.

As an example of similar abnormalities in the Group the following selected specimens can be cited in support:

- *Buegge* D101 (PERTH05399580); *G. anethifolia sens lat.*; hairs abnormally on some pedicels.
- *Preiss* 722 (MEL52538); *G. vestita* (Endl.) Meisn. subsp. *vestita*; hairs on pedicels.
- *Melville* 4140 (MEL98972; NSW621037); *G. triloba* Meisn.; hairs on pedicels.
- *P. Althofer* 178 (NSW125527); *G. anethifolia* R.Br.; scattered hairs on the dorsal surface of the ovary.

Morphology

Descriptive layout and morphological terminology follows Olde (2015), largely inspired by the extensive descriptions given by McGillivray and Makinson (1993). Inflorescence terminology was discussed by Olde and Marriott (1993) and Makinson (2000: 11). The term super-conflorescence was introduced by the latter but branched conflorescences is preferred here, the various inflorescence units of which are here termed unit conflorescences. Petiole terminology follows Hickey (1973). Petioles described as 3-merous, have a central vein (which may extend down the branch at the point of attachment or not, and two lateral veins that spread widely or scarcely at all. Floral branches refer to branches of a shrub on which conflorescences aggregate preferentially cf. leafy branches. The term *buds* alludes to conflorescence buds discussed by Olde and Marriott (2009). Although rhizomatous plants generally reproduce asexually, the presence of occasional fertile fruits (seed facultative) is a diagnostic feature worthy of taxonomic note.

Key to species of the *Triloba* Group with hairy outer perianth surfaces

A Plant habit monomorphic; all leaves similar and with the undersurface fully enclosed by margins; floral branches absent ..... ***G. erinacea***

A* Plant habit dimorphic; leaves polymorphic, reduced on floral branches, most with the undersurface exposed; floral branches usually present ..... B

B Generative habit seed-obligate; habit spindly, erect, 1.5–1.8 m high; style scarcely dilated above the stylar constriction; pollen-presenter fusiform with straight sides ..... ***G. metamorpha***

B* Generative habit rhizomatous; habit bushy, spreading, 0.5–0.8 m high; style prominently dilated above the stylar constriction; pollen-presenter broadly ovoid usually with convex sides ..... ***G. trichantha***

Taxonomy

Grevillea trichantha Olde, **sp. nov**.

Type: Western Australia: 2.1 km east of Brand Highway on Marchagee Track, *P.M. Olde, N. Marriott & K. Alcock* 01/134, 9 Sep 2001 (holo: NSW1099549; iso: CANB, K, MEL, PERTH).

Diagnosis: *Grevillea trichantha* is most similar to *Grevillea metamorpha* Makinson but differs in its low-growing (v. spindly, erect) habit of growth and rhizomatous generative (*v*. seed-obligate) habit; mature leaves generally smaller, 0.5–1.5(–1.8) cm long, usually tripartite with lateral lobes (*v*. 1.4–2.4 cm long, obovate-cuneate and apically dentate); stylar dilation ovoid, abruptly widened to *c*. 0.5 mm above a narrow constriction zone (*v*. stylar dilation very narrowly ovoid, scarcely swollen, to 0.3 mm wide); pollen-presenter bulbous-conical with convex sides (*v*. pollen-presenter subfusiform, narrowly truncate-conical to subcylindrical with straight sides).

Seedlings not seen. *Mature plant* a low-growing, dimorphic, rhizomatous, seed facultative, probably self-compatible *shrub* 0.5–0.8(–1.2) m high, 1–1.5 m wide, bushy at base with multiple ascending to spreading columnar floral branches. *Branchlets* 0.5–1 mm thick, terete, sericeo-tomentose, sometimes subvillous. *Ramet leaves* (basal leaves on root-suckers) (*Olde 01/134d*) 2.5–4 cm long, 1 cm wide, coarsely pinnatifid. *Adult leaves* 0.5–1.5(1.8) cm long, 5–12 mm wide, polymorphic, becoming gradually reduced on floral branches below and in the flowering zone; vegetative leaves crowded, sessile or very shortly petiolate, spreading to ascending, obovate in gross outline, flat to slightly secund, most usually coarsely 3–7-fid to biternate, the primary lobes deeply -sect or -fid; leaves on flower-bearing branchlets trifid to trisect in the distal 10 cm, with occasional lobes secondarily divided; *new growth* coppery-green, tomentose-villous; *leaf base* narrowly cuneate; *primary lobes* 3–5, ascending; *central lobe* usually bifid or trifid, sometimes deeply bi-lobed or bi-sect; *ultimate central lobes* 1.5–10 mm long, (0.7–) 0.8–2.2 mm wide, ascending, triangular to broadly triangular on vegetative leaves, linear or very narrowly triangular on floral branches, flat (sometimes slightly divaricate on floral branches); *lateral lobes* either simple or one or both either secondarily bi- or tripartite; *ultimate lateral leaf lobes* 0.3–1 cm long, 0.7–0.8 mm wide, spreading, linear to obovate-trifid, triangular; *apices of lobes* acute, spinescent, pungent; s*pine* 0.3–1.5 mm long, black with yellow base, straight or shortly curved; *margins* smoothly recurved to angularly revolute on smaller or reduced leaves, angularly refracted about the intramarginal vein on larger leaves; *adaxial surface* irregular, convex to concave, sometimes with depressions at the sinuses, glabrous or openly sericeous and soon glabrescent, the midvein scarcely evident, secondary veins and intramarginal veins faintly evident to obscure; *abaxial surface* mostly exposed, densely white sericeous except the veins subglabrous, prominent; *texture* coriaceous; *petioles* 0–0.2 mm long, 0.3 mm wide, normal, 3–merous, the medial axis not extending down the branchlet, the lateral veins scarcely spreading; adaxial surface concave, sparsely to moderately sericeo-tomentose, usually with scattered appressed short hairs; abaxial surface convex, pubescent to glabrous. *Conflorescences* simple or branched, usually axillary, occasionally subterminal on short side branches, not exceeding the leaves, mostly confined to the upper axils; *subterminal conflorescences* simple to 4-branched, *axillary conflorescences* simple to 4-branched; *unit conflorescences* 1 cm long, 1–1.2 cm wide,, subglobose, 14–20- flowered, acropetal; *buds* 1–2 mm long, usually pedunculate, globose, not overarched by bractiform leaves, development not arrested; *peduncles* 0.1–3 mm long, sericeous; *floral rachises* 4–8 mm long, 0.3–0.4 mm wide, white sericeo-tomentose, the hairs not to scarcely exceeding the rim of the nodes, slightly tapered distally; *involucral bracts* not seen; *common bracts* 0.6–1 mm long, 0.6–1 mm wide, sparsely sericeous outside, glabrous inside, ovate-acuminate, caducous at early bud stage. *Flower colour* pedicels white to creamy; perianth white with grey to dull yellow limb; pistils white, the pollen-presenter ageing purplish-pink after anthesis. *Flowers* acroscopic, not nectariferous, fragrance not noted, entomophilous; *pedicels* 5–7 mm long, 0.2–0.3 mm wide, sparsely sericeous, the apex gradually but slightly expanded, ascending, straight, not crowded; *basal pedicels* 5–7 mm long; *distal pedicels* 5–6 mm long; torus 0.7 mm wide, scarcely wider than the apex of the pedicel, transverse to slightly oblique; nectary absent to obscure and rising *c*. 0.1 mm above the toral rim, U-shaped with entire margin. *Pistil* 3.5–4 mm long, glabrous; *gynophore* 1.5–1.8 mm long; *ovary* 0.5 mm diam., round in side-view, compressed, remaining smooth after fertilisation; *stylar constriction* 0.2–0.4 mm long, 0.2 mm wide, incurved; *stylar swelling* 0.8–1 mm long, 0.35–0.5 mm width, tapering to 0.3 mm slightly below the style–end, ovoid; *pollen–presenter* 0.5–0.6 mm long, broadly conical with convex sides, the *base* 0.4–0.6 mm wide, abruptly divergent from, to gradually merged with, the style-end, straight to slightly oblique at *c*. 10°, not rimmed; *stigma* (0.1–)0.2 mm wide, oblique. *Perianth* (just before anthesis) 3–3.5.mm long, 0.5–1 mm wide, actinomorphic; *perianth tube* white in bud, 2–2.5 mm long, 0.5–1 mm maximum width, narrowly obovoid, contracting below the limb into a neck 0.5 mm wide; cylindrical, glabrous inside or sometimes a few scattered minute trichomes just above the base on each tepal or rarely sparsely pilose adjacent to the ovary; *perianth limb* 1–1.2 mm long, 1.2–1.5 mm wide, depressed globose to spheroidal, not ribbed; *tepals* 3–3.5 mm long, 0.3 mm wide at base, 0.5 mm wide in upper half, 0.2 mm wide below the limb; abaxial surface sericeous to sericeo-tomentose, sometimes the hairs only scattered on mature flowers, sometimes becoming glabrescent; adaxial surface glabrous or a few scaly simple trichomes 0.1–0.2 mm long at base, elsewhere papillose and usually farinaceous, the midrib obscure; *tepal-limbs* 1–1.2 mm long, 1 mm wide, the midrib obscure. *Fruits* follicular,

monospermous, 10 mm long, 6 mm wide, oblong-ellipsoidal, transverse to very oblique on incurved pedicel with attachment subposterior, 2–3 mm from base on dorsal side; *fructual style* oblique; *fructual pollen-presenter* conical; *pericarp* 0.5–0.7 mm thick along the suture, thicker at the ends; *exocarp* smooth; *mesocarp* crustaceous; *endocarp* smooth. *Seeds* not seen. (Figures 1, 2)

Fig. 1. a. Flowering branchlet of *Grevillea trichantha*. b. New growth of *Grevillea trichantha*. c. *Grevillea trichantha* in natural habitat. Photos: a, c by P.M. Olde; b by I. Gilmour.

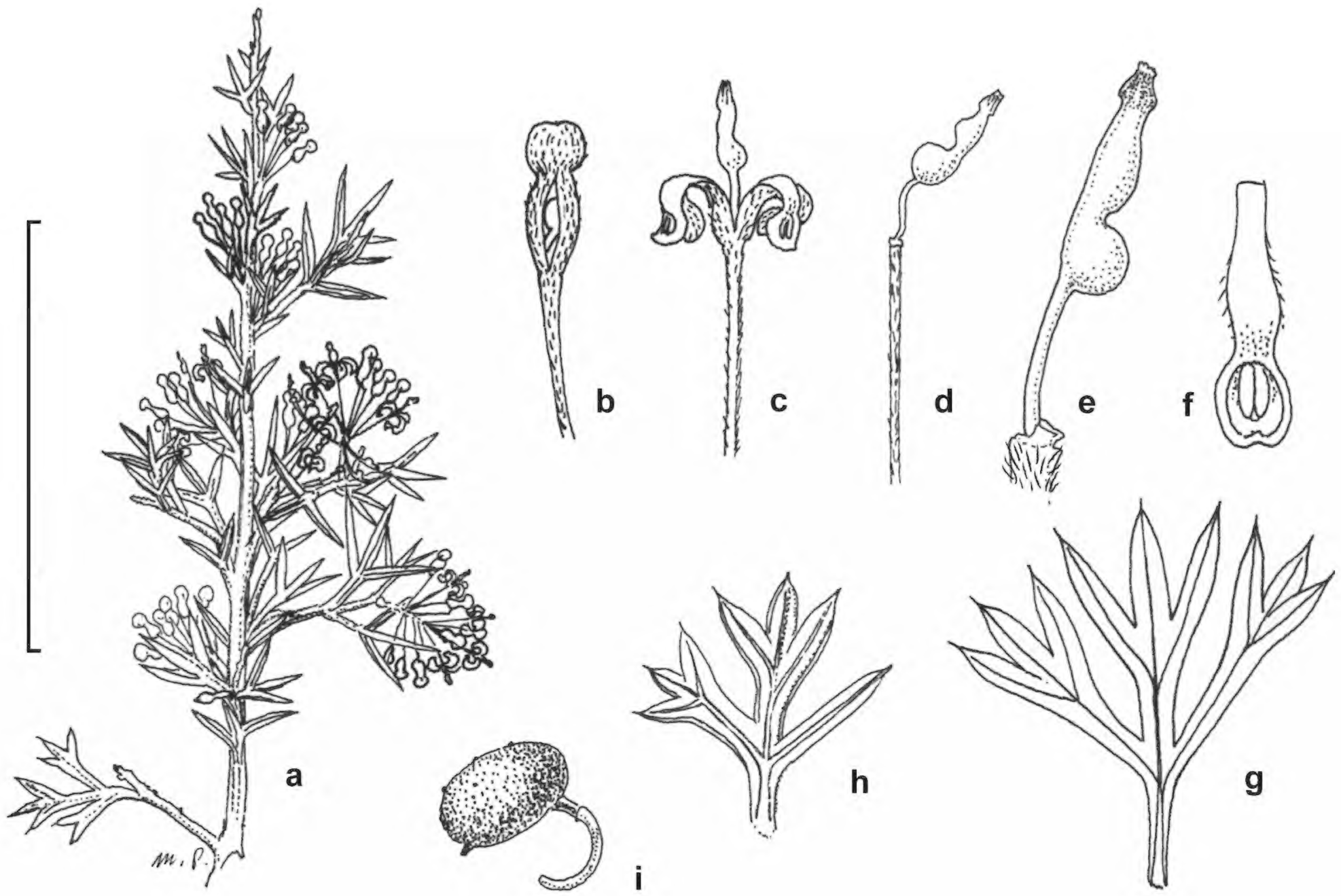

Fig. 2. *Grevillea trichantha*. a. Habit. b. Flower bud before anthesis. c. Flower after anthesis. d. Flower without perianth. e. pistil. f. Tepal inner surface. g, h. Leaf variants. i. Follicle. Scale bar: a = 50 mm; b, c = 12.5 mm; d = 10 mm; e, f. = 5 mm; g, h = 25 mm; i = 33 mm. Illustration: M. Pieroni; modified for publication by L. Elkan.

Diagnostic characters: Low-growing, rhizomatous, dimorphic habit, bushy at base. Mature leaves usually coarsely bipinnatifid; floral branches with sessile, highly reduced trisect leaves, often with secondary division; leaves flat or secund with under-surface exposed and densely sericeous. Conflorescences simple or few-branched, axillary or subterminal, shortly pedunculate; peduncles, floral rachises, outer surface of common bracts, pedicels, and outer surface of perianth sparsely to densely sericeous; floral rachises 4–8 mm long; pedicels 5–7 mm long; common bracts 0.6–1 mm long, 0.6–1 mm wide; nectary obscure to scarcely evident; pollen-presenter ovoid- to bulbous-conical with convex sides; perianth actinomorphic; fruits rare, follicular with smooth exocarp.

Distribution: Western Australia, where known to date only from the type locality in the Coorow LGA. It occurs in the South-west (SW) Botanical Province(s), in the Lesueur Sandplain Subregion of the Geraldton Sandplains IBRA Region.

Phenology: Flowering occurs mainly in Spring with spasmodic flowering at other times, mainly in response to increased rainfall. Fruits, which set rarely, have not been collected when mature.

Habitat and ecology: Flat to undulating terrain. Grows in dense, mixed Proteaceae heath with *Adenanthos* sp., *Banksia candolleana*, *B. nivea*, *B. tridentata*, *B. incana* var. *brachyphylla*, *B. sphaerocarpa*, *Conospermum* sp., *Grevillea eriostachya*, *G. saccata*, *G. shuttleworthiana* subsp. *canarina*, *G. uncinulata sens lat.*, *Hakea recurva*, *H. eneabba*, *Lambertia* sp., *Stirlingia* sp. and *Synaphea* sp. Other associated species include *Eucalyptus todtiana*, *Eremaea* sp., *Hibbertia* sp. and *Verticordia grandis*. Soils are white gravelly sand. Elevation ± 220–230 m asl.

Conservation status: Grows in a scattered roadside population spread over *c.* 1 km to the east of the Brand Highway. A conservation code of Priority One is recommended.

Etymology: *Gk. trich-* hairy, *anthos-* flower, in reference to the hairy floral organs of this species.

Discussion: (*Grevillea trichantha* is one of only three species in the *Triloba* group with hairs on the floral organs. The other two, *G. erinacea* and *G. metamorpha*, differ in their seed-obligate generative habit. *Grevillea erinacea* further differs in its monomorphic leaves, all of which have linear-subulate lobes with strongly revolute margins that fully enclose the leaf abaxial surface up to the midvein.) Differences from *G. metamorpha,* a

very rare species with 15 plants counted in a 2015 post-fire survey by the author, are outlined above (and see fig. 3). Both *Grevillea trichantha* and *G. metamorpha* exhibit a similar pattern of leaf reduction from broad basal vegetative leaves to trisect, xeromorphic leaves on the floral branches. The specimen of *G. metamorpha* (*Olde 99/131a*) also has hairs behind the anthers, a feature not seen elsewhere in the *Triloba* Group. All three species occur in the same IBRA region of south-west Western Australia.

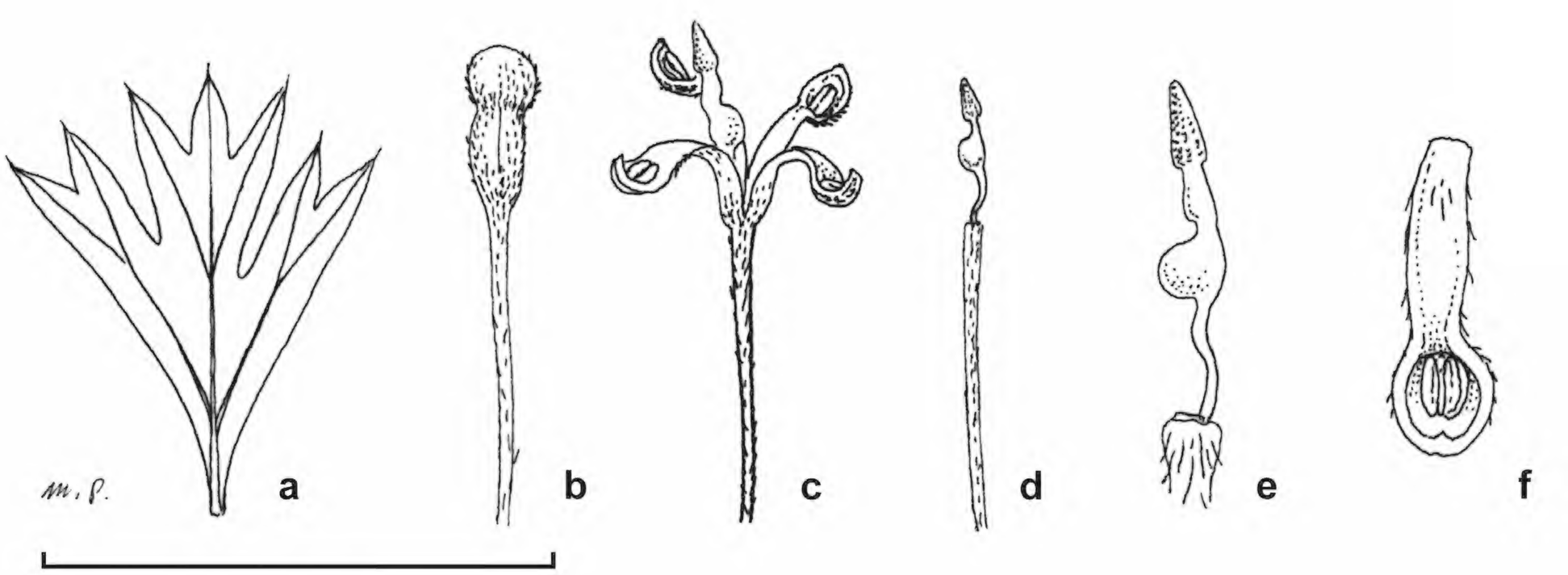

Fig. 3. *Grevillea metamorpha*. a. Leaf. b. Flower bud before anthesis. c. Flower after anthesis. d. Flower without perianth. e. Pistil. f. Tepal inner surface. Scale bar: a = 25 mm; b, c, d = 12.5 mm; e, f. = 6.25 mm. Illustration: M. Pieroni; modified for publication by L. Elkan.

Selected specimens: WESTERN AUSTRALIA: Marchagee Track, 0.8 km west of Mazza Road, Badgingarra, north side of track, *P.M. Olde 01/46, K. Alcock & N. Marriott,* 31 Aug 2001 (AD, CANB, K, MEL, NSW); Marchagee Track, 0.7 km west of Mazza Road, Badgingarra, south side of track, *P.M. Olde 01/48, K. Alcock & N. Marriott,* 31 Aug 2001 (CANB, NSW, PERTH); Marchagee Track, 1.9 km east of Brand Highway, gravel pit *c.* 50 m north of track, *P.M. Olde* 02/94 & N. Marriott, 7 Sep 2002 (NSW, PERTH); Between 0.3–1 km west of Mazza Rd. on Marchagee Track, *P.M. Olde 13/217 & G. Meiklejohn*, 29 Aug 2013 (MEL, NSW, PERTH).

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References

Hickey LJ (1973) Classification of the architecture of dicotyledonous leaves. *American Journal of Botany* 60: 17–33. https://doi.org/10.1002/j.1537-2197.1973.tb10192.x

McGillivray DJ, Makinson RO (1993) *Grevillea* Proteaceae. (Melbourne University Press: Carlton, Victoria)

Makinson RO (2000) *Proteaceae 2*, Grevillea. *Flora of Australia Volume 17A*. (CSIRO Publishing: Melbourne)

Meisner CF (1855) New Proteaceae of Australia. *Hooker's Journal of botany and Kew Garden miscellany* 7: 65–78. https://www.biodiversitylibrary.org/item/6325#page/67/mode/1up

Olde PM (2015) *Grevillea laurifolia* subsp. *caleyana* Olde (Proteaceae: Grevilleoideae: Hakeinae), a new subspecies from the Blue Mountains of New South Wales, Australia. *Telopea* 18: 97–108. https://dx.doi.org/10.7751/telopea8309

Olde PM (2017) A preliminary checklist of fossil names in extant genera of the Proteaceae. *Telopea* 20: 289–324. https://dx.doi.org/10.7751/telopea10644

Olde PM (2020) *Grevillea pieroniae* Olde (Proteaceae: Grevilleoideae: Hakeinae), a rare new species in the *Triloba* Group from the Stirling Range, Western Australia, and a short history of the group. *Telopea* 23: 227–235. http://dx.doi.org/10.7751/telopea14783

Olde PM (2021) *Grevillea hortiorum* Olde (Proteaceae: Grevilleoideae: Hakeinae), an uncommon species from winter-damp woodlands in the Avon Wheatbelt, south-west Western Australia. *Telopea* 24: 1–6. http://dx.doi.org/10.7751/telopea14823

Olde PM, Marriott NR (1993) A taxonomic revision of *Grevillea angulata* (Proteaceae: Grevilleoideae and closely related species from the Northern Territory and Western Australia. *Telopea* 5: 399–417. http://dx.doi.org/10.7751/telopea19934984

Olde PM, Marriott NR (2009) *Grevillea tetragonoloba* recircumscribed, with notes on its typification and a new segregate species from south-west Western Australia, *Grevillea nivea* (Proteaceae: Grevilleoideae), described. *Nuytsia* 19(2): 229–243.

Olde PM, Marriott NR (2021) *Grevillea merceri* Olde & Marriott (Proteaceae: Grevilleoideae: Hakeinae) an uncommon, geographically isolated species in the *Triloba* Group from subcoastal areas of southern Western Australia. *Telopea* 24: http://dx.doi.org/10.7751/telopea14797

Venkata Rao C (1964) Pollen grains of *Grevillea vestita* Meissn. *Current Science* 33: 722–724. https://www.jstor.org/stable/24065948

Venkata Rao C (1966) Studies in the Proteaceae VIII. Morphology, floral anatomy and embryology of *Grevillea* R.Br. *Proceedings of the National Institute of Sciences of India* 33(B): 163–199.

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Progress towards resolution of the *Indigofera monophylla* complex (Fabaceae: Faboideae)

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Abstract

The application of the name *Indigofera monophylla* is clarified by reference to the type held in the Geneva herbarium and a revised description provided. The name has been widely applied to plants with rounded, unifoliolate leaves and some workers have suggested that there are multiple species within this broadly defined group. One of these, with restricted distribution within the Pilbara bioregion, has previously been given the phrase name *Indigofera* sp. Bungaroo Creek (S. van Leeuwen 4301) and is formally named here as *Indigofera rivularis* Peter G.Wilson. Two additional species in this complex are also described: *Indigofera deserticola* Peter G.Wilson & Rowe, is a species of sandplains occurring within the Great Sandy Desert and Dampierland Bioregions, and *Indigofera rotula* Peter G.Wilson, which is a species with smaller leaves and flowers that occurs primarily in areas south of the Pilbara. A key to these species is provided.

Introduction

In recent works on Australian species of *Indigofera* (Wilson & Rowe 2004, 2015), *I. monophylla* DC. has been noted to be an extremely variable taxon in need of revision. Variation between plants in this group are primarily seen in habit, from semi-prostrate to erect, in leaf indumentum, from densely white-tomentose to sparsely appressed-hairy, calyx indumentum, from dark brown to grey-white, as well as in flower colour, varying from deep red to pale red. Additionally, the plants have been recorded from many different habitats, including sandplains and dunes, along sandy or stony seasonal watercourses and adjacent floodplains, on rocky ranges and slopes, and on limestone or granite substrates.

Binks et al. (2016) conducted a genetic analysis of *Indigofera monophylla* within the Pilbara region, one of six taxa within the region that were assessed for suitability as seed sources for post-mining land rehabilitation. Their study found that sampled populations of the *I. monophylla* complex in that region "exhibited moderate levels of differentiation and formed three genetic clusters", one of which ('Cluster Three') was strongly genetically distinct from the other two. Examination of the type of *Indigofera monophylla*, as discussed below, clearly showed that it is representative of populations in genetic 'Cluster One' of Binks et al. (2016).

Examination of specimens has resulted in confirmation of specific rank for the taxon informally known as *Indigofera* sp. Bungaroo Creek (S. van Leeuwen 4301) (Western Australian Herbarium 1998–), and recognition of a further two new species. The first of these occurs on sandplains to the north and west of the Pilbara and very likely includes the two specimens that comprise 'Cluster Three' in the analysis of Binks et al. (2016).

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The second new taxon has previously been recognised as distinct and occurs south of the Pilbara in shrubland, sometimes adjacent to watercourses but often near low, granite outcrops. Even after recognition of these segregates, *Indigofera monophylla* remains as a variable taxon. This is supported by the genetic structure of clusters 'One and Two' in the study of Binks et al. (2016).

Key to species in the *I. monophylla* group

1. Leaflet veins prominent below, often impressed above ..... ***I. monophylla***
1. Leaflet veins obscure to somewhat prominent below 2
2. Stipules short , triangular, 1–2 mm long; staminal tube 5.5–6.5 mm long..... 3
2. Stipules slender, 3–4.5 mm long; staminal tube 4–4.5 mm long ..... ***I. rotula***
3. Leaflet ovate to elliptical, silvery-grey to green; indumentum dense, appressed..... ***I. deserticola***
3. Leaflet rounded, pale green-grey; indumentum sparse ..... ***I. rivularis***

Taxonomy

Indigofera monophylla DC., Prod. 2: 222 (1825)

Type citation: '? in Novae Hollandiae orâ orientali'

Holotype: Nouvelle Hollande, côte orient (G-DC, barcode G00497797, Fig. 1). Isotype: P, barcode P00298010.

Erect to prostrate shrub or subshrub, 0.2–1 m high, with woody rootstock; young stems terete to ridged, usually grey-white, sometimes new growth distinctly rusty-brown, strigose or tomentose with dense to very dense, appressed to spreading, equally biramous hairs. Leaves unifoliolate with point of articulation; stipules narrowly triangular, (1–)1.5–3.5 mm long, not spinescent, usually persistent; petiole (3.5–)6–8.5(–10.5) mm long; rachis furrowed, often slightly; multicellular hairs at point of articulation, few, short and dark. Leaflet with small to conspicuous stipellae to 0.5 mm long; lamina obovate to orbicular, 10–40 mm long, (8–)10–25(–33) mm wide; upper surface grey to white with rather dense, appressed to spreading hairs; lower surface grey to white with appressed to spreading hairs; apex obtuse and mucronate; veins often impressed above and prominent below. Inflorescences 55–150 mm long, equal to, or longer than the leaf; peduncle 8–24 mm long; bracts triangular 1–2.5(–4) mm long; flowers red to deep red or maroon; pedicel c. 0.5mm long. Calyx 2–3(–4.5) mm long, with unequal to subequal lobes less than to longer than the length of the tube and dense, white or brown, appressed hairs. Standard ovate, (5.5–)7–9 mm high, 4–6 mm wide, the back densely clothed with appressed, coppery (rarely white) hairs. Wings spathulate, 5.5–6.5 mm long, 2–3 mm wide, ±glabrous. Keel 7–9 mm long, 2–3 mm deep; lateral pockets 0.7–1.5 mm long; apex acute, hairs moderately dense to dense, golden brown, at the tip and along the bottom; margins ciliate. Staminal tube 4.5–5.5(–7) mm long, pigmented. Ovary moderately to densely hairy. Pod spreading to descending, terete, 17–32 mm long, 2–3 mm deep, grey, hairs moderately dense to dense, appressed; apex pointed; endocarp spotted; seed 4–8 per fruit.

Typification: The type citation reflects the wording on the tag attached to the specimen in the de Candolle herbarium (G-DC) at Geneva, although the origin of the collection is incorrectly marked as the east coast ('côte orient'). The specimen tag also notes that it was received from Paris ("mus. de Paris") in 1821. In the Geneva archives (Candolle 1830) it is recorded that de Candolle received, in August 1821, 220 duplicates from Paris mentioned as "pl. de Nouvelle Hollande (voy. Baudin)" (M. Callmander pers. comm.). The corresponding sheet at P, P00298010, is a duplicate of this and is, therefore, an isotype. No other duplicates were located at G (fide M. Callmander).

The isotype at P is labelled 'Leschenault, Ile des Amiraux', and would have been collected on 27 July 1801 by a party sent from the *Géographe* to explore that island. The name 'Ile des Amiraux' had been chosen by Baudin but it was subsequently changed to Depuch Island by Peron after Baudin's death in Mauritius in 1803 (https://slwa.wa.gov.au/freycinet/depuch-island).

Notes: As accepted here, this taxon varies in habit from a low-growing multi-stemmed subshrub to a shrub up to c. 1 m high. It shows a range of variation in leaf size and morphology, with one specimen (*Nordenstam & Anderberg 306*) approaching *I. rugosa* Benth. in colour and density of indumentum and with inflorescence bracts and sepals longer than usual.

Figure 1. Holotype of *Indigofera monophylla* in the de Candolle herbarium, Geneva.

Other specimens have quite small leaves (*Wilson 1715* and *van Leeuwen 1813*) but these forms are geographically widely separated, suggesting that this feature is likely due to environmental factors. The genetic diversity underlying this observed variation in the Pilbara is amply demonstrated in Figure 10 of Binks et al. (2016) and Pilbara specimens from areas occupied by individuals of 'Clusters One and Two' in that study are included in the concept of *Indigofera monophylla*.

Conservation status: Not at risk.

Distribution and habitat: Western Australia: occurs mostly in the Pilbara Bioregion, north to the southern Kimberley with some extension south into the Carnarvon, and Gascoyne Bioregions (IBRA, 2012).

The species has been found on rocky hills on limestone and ironstone substrates, but also on loamy plains, and adjacent to watercourses. It is perhaps endemic to Western Australia but the possible relationship between the Pilbara populations and the few disjunct Northern Territory records from rocky substrates cited below (e.g, *Maconochie 707*; *Winkworth 430*) should be investigated. Connectivity between the Pilbara and southern parts of the Northern Territory is interrupted by the Gibson and Little Sandy Desert Bioregions, so the time of separation of the sites is likely to have been considerable.

Phenology: Flowering has mostly been recorded from late Autumn to early Spring.

Selected specimens (coast and offshore islands): Western Australia: Depuch Island, NW of Roebourne, *Royce 7078*, 28 May 1962 (PERTH 02809664); Watering Valley, Depuch Island, *Royce 7117*, 29 May 1962 (PERTH); Dolphin Island, Dampier Archipelago, *Royce 7204*, 5 June 1962 (PERTH); Barrow Island, *Butler 10*, 17 Aug 1973 (PERTH); 21 km S of Whim Creek, *Wilson 329*, 7 Jun 1988 (NSW, AD, PERTH).

Other selected specimens: Western Australia: Great Northern Highway, c. 25 km W of Wolfe Creek turn-off, *Wilson 868 & Rowe*, 31 Aug 1991 (NSW, K, L, PERTH, RSA); 62 miles SW of Halls Creek, *Byrnes 2222*, 21 May 1971 (DNA, CANB, NSW, PERTH); Mt Fairburn, ESE of Fitzroy Crossing, *Bennett 1985*, 30 May 1967 (PERTH); Edgar Range, SE of Broome, *Kenneally 5541*, 9 Aug 1976 (CANB, PERTH); 33.3 km S of "Wallal Downs" turn-off, Great Northern Highway, *Wilson 897 & Rowe*, 4 Sep 1991 (NSW, E, PERTH, PRE); 52.6 km N of Shay Gap, *Wilson 898 & Rowe*, 4 Sep 1991 (NSW, PERTH); Near Wittenoom, *Gittins 1479*, Aug 1967 (NSW, CANB); Great Northern Highway, 21.3 km N of Yandeyarra turn-off, *Wilson 1715*, 30 May 2006 (NSW, AD, CANB, DNA, PERTH); Doolena Gap, George Range, *Wilson 998 & Rowe*, 8 Sep 1991 (NSW, K, PERTH); 70 km SE of Karratha on Robe River rail access track, *Mitchell 1854*, 17 May 1991 (PERTH, NSW); Gregory Range; opposite abandoned mine, *Wilson 945 & Rowe*, 5 Sep 1991 (NSW, PERTH); 6.1 km East of Oakover River Crossing of the Marble Bar–Telfer Rd, *Albrecht 11088*, 25 Aug 2004 (DNA, NSW); Millstream Station, *Beard 4544*, 17 Aug 1966 (PERTH); Mt Herbert, Chichester-Millstream NP, *Nordenstam & Anderberg 306*, 4 Oct 1989 (PERTH); Python Pool, east side of Mount Herbert, *Briggs 3651*, 17 Jun 1970 (NSW); 5 km from Mt Florence Homestead on track to the upper Sherlock River, *Mitchell PRP 1465*, 3 Sep 1996 (NSW, PERTH); Great Northern Highway, 9.2 km S of Bea Bea Creek, *Wilson 1732*, 1 Jun 2006 (NSW, AD, CANB, DNA, PERTH); Cape Range–Rough Range at 20.0 km on road to coast from Learmonth, *Briggs 8812 & Johnson*, 6 Aug 1991 (NSW, L, MEL, MO, PERTH); Bee Gorge, Hamersley Range, *Wilson 1068 & Rowe*, 12 Sep 1991 (NSW, PERTH); Saddle of Drillers Ridge, *van Leeuwen 1061*, 24 Sep 1991 (NSW, PERTH); Barlee Range Nature Reserve, 9.7 km W of Mount Palgrave, *van Leeuwen 1369*, 5 Aug 1993 (NSW, PERTH); Barlee Range Nature Reserve, SW of Jarradubundy Bore, *van Leeuwen 1813*, 21 Jun 1994 (PERTH, NSW); Towera Station, *Cranfield 1771*, 5 Aug 1981 (PERTH); Rocky Pool, Gascoyne River, *Kenneally 4667*, Oct 1975 (CANB, PERTH).

Northern Territory: Central Mount Stuart, *Maconochie 707*, 26 June 1969 (AD, DNA, NSW); Vaughan Springs, *Winkworth 430*, 4 July 1954 (CANB); Laura Vale, *Tietkens s.n.*, 24 May 1889 (AD, DNA, MEL).

Indigofera deserticola Peter G.Wilson & Rowe, **sp. nov.**

Diagnosis: Differs from *Indigofera monophylla* by having stems and leaves that are silvery-grey to green with dense appressed hairs, leaflets with lamina ovate to elliptical, and short stipules.

Holotype: Western Australia: Dampier: Great Northern Highway, 49 km S of Thangoo turn-off, *Peter G. Wilson 883 & R. Rowe*, 3 Sep 1991 (NSW, barcode NSW245871). Isotypes: PERTH 2116855, B, L, MO.

Erect shrub, 0.6–1(–1.5) m high; young stems ridged, grey or yellowish-brown, strigose with dense to very dense fine, appressed, equally biramous hairs that persist on older stems. Leaves unifoliolate; stipules triangular, (0.5–)1–2 mm long, rarely longer, pubescent; usually persistent; petiole (1.5–)3–7 mm long, rachis slightly furrowed; multicellular hairs at point of articulation sparse to moderately dense, conspicuous, red to dark brown, club-shaped; stipellae (0.2–)0.5–1 mm long; lamina ovate to elliptical, (10–)15–30(–43) mm long, (5.5–)8–15(–24) mm wide, upper and lower surfaces silvery-grey to green, with moderately dense to dense appressed hairs; veins not prominent; apex obtuse and mucronate. Inflorescences 20–70(–85) mm long, equal

to, or longer than, the leaves; peduncle (1.5–)2–7(–10) mm long; bracts triangular (0.5–)1–2 mm long; flowers pink to purple; pedicel 0.7–1.5 mm long. Calyx (1.5–)2–3(–4.0) mm long, with subequal lobes shorter than, or equal to, the length of the tube and moderately dense, grey, appressed hairs. Standard pink to purplish, ovate to narrowly orbicular, 7.6–9.4mm high; (5.5–)6–7(–7.5) mm wide; apex obtuse and shortly mucronate, the back densely clothed with golden brown hairs. Wings narrow obovate, 7–8.5 mm long; 2.5–3 mm wide. Keel 8–8.9 mm long; 2.2–3 mm deep; lateral pockets 1.1–1.6 mm long; apex acute; hairs moderately dense, grey-brown at the tip and along the bottom. Staminal tube 5.5–6.5 mm long, pigmented. Ovary moderately hairy. Pod spreading to descending, terete, 14–28 mm long, c. 2–3 mm deep; hairs moderately dense to dense, appressed; apex pointed; endocarp spotted; seed 4–8 per fruit.

Etymology: From the Latin (plural) *deserta*, deserted places/deserts, and the suffix *-cola*, an inhabitant, a reference to the Great Sandy Desert where this species occurs.

Note: Given that there are specimens cited here from north of Nullagine (*Burbidge 1169* and *Burbidge 1171*), it is very likely that it was specimens of this taxon that comprised 'Cluster Three' in the study by Binks et al. (2016). Those authors suggested that the two samples in this cluster "may represent a separate taxonomic entity".

Conservation status. Not assessed but widespread and unlikely to be at risk.

Distribution and habitat: Western Australia: sand plains and Pindan country south of Broome, predominantly in the Dampierland and Great Sandy Desert Bioregions (IBRA, 2012) but also extending into the eastern Pilbara, far north eastern Gascoyne and Little Sandy Desert Bioregions. The extent of its distribution in desert areas is uncertain due to limited access. The status of collections of *I. monophylla sens. lat*. from the Northern Territory are uncertain as there are only a few collections at the margins of the Tanami and Gibson Deserts. However, one collection from east of the Northern Territory border (*Lang 5*) appears to represent this taxon.

Phenology: Flowering has been recorded from late Autumn to late Spring.

Selected specimens examined: Western Australia: Jigalong Depot, *Royce 1517, 1540*, 12 May 1947 (PERTH); Anketell Ridge, Great Sandy Desert, *Mitchell 1111*, 14 May 1979 (DNA); Edgar Range, SE of Broome, *Kenneally 5523*, 7 Aug 1976 (CANB, PERTH); 116 miles [c. 186 km] from Broome towards Port Hedland, *Gittins 1459*, Aug 1967 (NSW); c. 160 km south-southwest of Broome on Great Northern Highway, *Briggs 3654*, 17 Jun 1970 (NSW); 100 miles [c. 160km] N of Anna Plains, *Beard 4076*, 10 May 1965 (NSW); Great Northern Highway, 35.5 km S of Lagrange Mission turn-off, *Wilson 885 & Rowe*, 3 Sep 1991 (NSW, E, PERTH, PRE, US); 122 km from Broome towards Port Hedland along Great Northern Highway, *Telford 11736*, 15 May 1992 (NSW, CANB PERTH); Fortescue: S of Mt Edgar Station, Nullagine Road, *Burbidge 1169, 1171*, 12 Jun 1941 (PERTH); Carrowina Creek, *Wilson 959 & Rowe*, 6 Sep 1991 (NSW, PERTH); Near Rudall R., *George 10859*, 24 May 1971 (CANB, NSW, PERTH); Bore 4 m [6.4 km] W of N.T. border (50 m [80 km] W of Mongrel Downs), *Maconochie 989*, 20 Apr 1971 (DNA, NSW); Dovers Hills, *George 8984*, 27 July 1967 (NSW, PERTH); Djaluwon Creek, near S end of Lake Gregory, *George 15421*, 26 Apr 1979 (DNA, PERTH).

Northern Territory: Birrindudu Station, *Lang 5*, 22 Jul 1993 (DNA, NSW).

Indigofera rivularis Peter G. Wilson, **sp. nov.**

Diagnosis: Differs from *Indigofera monophylla* by its relatively tall, erect habit, generally shorter stipules, and sparse indumentum.

Holotype: Western Australia: Tributary of Cave Creek; gorge N of the Mount Brockman Road, Hamersley Range, *Peter G. Wilson 1795*, 10 Jun 2006 (NSW, barcode NSW988888). Isotypes: CANB, MEL 2435248A, PERTH.

Indigofera sp. Bungaroo Creek (*S. van Leeuwen 4301*), Western Australian Herbarium, in FloraBase, https://florabase.dpaw.wa.gov.au/search/current/20317 [accessed 29 April 2021].

Erect shrub, 1–2.5 m high; young stems ridged to terete, speckled with very dense, appressed white and brownish, strigose, equally biramous hairs. Leaves unifoliolate with point of articulation; stipules triangular, often narrowly, (0.5–)1–2 mm long, not spinescent, ± persistent; petiole (4–)5–10 mm long; rachis furrowed, often slightly; multicellular hairs at point of articulation moderately dense, usually conspicuous, red to dark brown, conical. Leaflet with inconspicuous stipellae 0.2–0.4 mm long; lamina broadly ovate, elliptical or orbicular; (15–)25–40(–60) mm long, 12–32 mm wide; upper surface grey-green with sparse, appressed hairs; lower surface grey-green with sparse, appressed hairs; apex obtuse and mucronate; veins not prominent. Inflorescences (35–)50–80(–100) mm long, longer than the leaf; peduncle 5–12 mm long; bracts narrowly triangular 1–2 mm long; flowers deep pink to red; pedicel 1.5–2 mm long, lengthening to c. 3 mm in fruit. Calyx (2.0–)2.8–3.6 mm long, with unequal lobes longer than the length of the tube and dense, grey to brown or golden-brown, appressed spreading hairs. Standard deep pink to maroon or red, broadly ovate, 7.5–8.5 mm high, 6–7 mm wide, the back densely clothed with golden-brown hairs. Wings spathulate, 6–7.5 mm long,

2–3.5 mm wide. Keel 6.5–8.5 mm long, 2–2.5 mm deep; lateral pockets 1.5 mm long; apex acute; hairs margins ciliate. Staminal tube 5.5–6.5 mm long, colourless or free ends and tube pigmented. Ovary moderately to densely hairy. Pod spreading to descending, ±terete, (23–)25–36(–40) mm long, 3–4 mm deep, brown; hairs short and somewhat crisped, moderately dense to dense, appressed; apex pointed; endocarp spotted; seed (4–)8–10 per fruit.

Etymology: The epithet is taken from the Latin *rivularis*, pertaining to small streams, and alludes to the frequent association of this species with rocky creeks that are tributaries of the Robe and Ashburton Rivers in the Pilbara.

Conservation status: Listed by Smith & Jones (2018) as 'Priority Three' under Department of Biodiversity, Conservation and Attractions Conservation Codes for Western Australian Flora, as *Indigofera* sp. Bungaroo Creek (S. van Leeuwen 4301) (Western Australian Herbarium 1998–). This level of listing indicates that the species is not believed to be under immediate threat but is nevertheless in need of further assessment.

Distribution and habitat: Western Australia: occurs in the Pilbara IBRA region, along rocky creek-lines in open low woodland of eucalypts and Acacias on ironstone substrates.

Phenology: Flowers May to July.

Selected specimens examined: Western Australia: Duck Creek, out from Mt Brockman, *Blockley 311*, 9 July 1966 (CANB, PERTH); c. 9 km along Duck Creek track off the Nanutarra–Paraburdoo road, *Peter G. Wilson 1103, 1104 & R. Rowe*, 14 Sep 1991 (NSW, PERTH); about 22 km W from Hamersley Hsd, just N of road to Brockman, *Mitchell PRP 1053*, 13 May 1996 (NSW, PERTH); 12.8 km ESE of Mount Rica, 32.2 km SW of Mt Elvire, 39.5 km NNW of Mt Farquhar, Hamersley Range, *van Leeuwen 4301*, 13 Oct 1998 (NSW, PERTH); West of Bungaroo Creek, Western Hamersleys, *Mitchell 10567 & Newland*, 16 Oct 2014 (NSW, PERTH); Headwaters of the Robe River, Hamersley Plateau, *Mitchell 10042 & Holm*, 18 Jul 2011 (NSW, PERTH); Yathalla Creek, near Mt Rica, *Gardner 6389*, 22 Oct 1941 (PERTH).

Indigofera rotula Peter G. Wilson, **sp. nov.**

Diagnosis: Differs from other species in the *Indigofera monophylla* group by its generally smaller leaves with spreading hairs (particularly on the undersurface), longer stipules, and smaller flowers (staminal tube to 4.5 mm long) with relatively long sepals.

Holotype: Western Australia: Austin: 0.5 km E of Aleenya Well, Yarlarweelor Station, *Cranfield 5594*, 10 Aug 1986 (PERTH). Isotype: NSW, barcode NSW 1101902.

Shrub or subshrub 0.25–1 m high; young stems terete, moderately densely hairy with white to grey, dense equally biramous hairs, sometimes with ascending arms. Leaves unifoliolate with point of articulation; stipules slender, (1.5–)3–4.5 mm long, ±persistent, with marginal and axillary red to dark brown, club-shaped multicellular hairs, petiole 2.5–4.5 mm long; rachis hairy, obscurely furrowed; multicellular hairs at point of articulation few; petiolule 0.6–1.4 mm long. Leaflet with small stipellae 0.6–1.5(–2.5) mm long; lamina ovate to broadly elliptical, 9.5–16 mm long, 7.5–13 mm wide; upper surface grey with moderately dense, appressed to slightly spreading hairs; lower surface paler grey, the hairs often more flexuose; apex obtuse and mucronate; veins slightly impressed above, raised but not prominent below. Inflorescences 20–50(–60) mm long, longer than the leaf; peduncle 9–10(–15) mm long; bracts narrowly triangular 1.5–2 mm long, ±persistent till anthesis; flowers red; pedicel 0.5–1 mm long. Calyx to 2.5 mm long, clothed with dense, dark brown appressed hairs; lobes unequal to subequal, longer than the length of the tube. Standard red, ovate to orbicular, 4.5–6.5 mm high, 4–5 mm wide, the back densely clothed with dark hairs. Wings paler, spathulate, 4.5–5 mm long, 1.5–2 mm wide. Keel red, 6–6.2 mm long, 2.5 mm deep; lateral pockets 1–1.3 mm long; apex obtuse to rounded; hairs sparse, along the bottom towards the tip; margins ciliate. Staminal tube 4–4.5 mm long, pigmented. Ovary moderately to densely hairy. Pod spreading to descending, terete, 21–25 mm long, 2.5–3 mm deep, grey to brown, strigose to tomentose; hairs moderately dense to dense, appressed to spreading; apex pointed; endocarp spotted; seed c.7 per fruit.

Etymology: From the Latin *rotula*, a little wheel, with reference to the smaller, rounded laminae. The epithet is a noun in apposition.

Conservation status: Not assessed.

Distribution and habitat: Western Australia: mostly south of the Pilbara Bioregion, in the Carnarvon, Gascoyne and Murchison Bioregions (IBRA, 2012). Recorded as occurring in shrubland, sometimes adjacent to watercourses or near low, granite outcrops. Recorded in flower from late Autumn to early Spring

Selected specimens examined: Western Australia: near Lake Austin, *Peipers s.n.*, 1895 (MEL565583); 17 miles W of Kalli, *Gardner 14512*, 30 Aug 1963 (PERTH); East of Kalli Homestead, *Wilson 1167 & Rowe*, 19 Sep

1991 (NSW, PERTH); Pettiford Pool, Garden Gully Creek, *Wilson 1147 & Rowe*, 18 Sep 1991 (NSW); 100 m N of Yoothapina turn-off, Great Northern Highway, *Wilson 1150 & Rowe*, 18 Sep 1991 (NSW, PERTH, PRE); Carnarvon road [North West Coastal Highway], *Demarz 3337*, 14 Aug 1971 (PERTH); Gifford Creek Station, *Wilcox Q145*, 7 Jul 1970 (PERTH); 1 km WSW of Deep Yunda Bore, Milly Milly Station, *Cranfield 5323*, 24 Apr 1986 (PERTH); Peak Hill road, *Brockway 17*, May 1953 (PERTH); Ullawarra Station, *Royce 6504*, 17 Aug 1961 (PERTH).

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References

Binks R, Byrne M, Coates D, van Leeuwen S (February 2016) *Pilbara Provenance Project*. Unpublished final report, Science and Conservation Division: Perth, Western Australia.

Candolle AP de (1830) *Catalogue de l'herbier d'après les époques et les origines des échantillons qui le composent*. Private collection de Candolle, Geneva.

IBRA (2012) Australia's Bioregions, version 7. https://www.environment.gov.au/land/nrs/science/ibra/australias-bioregions-maps [accessed 3 Mar 2021]

Smith MG, Jones A (2018) Threatened and Priority Flora list 5 December 2018. Department of Biodiversity, Conservation and Attractions: Kensington, Western Australia. https://www.dpaw.wa.gov.au/plants-and-animals/threatened-species-and-communities/threatened-plants [accessed 18 March 2021]

Western Australian Herbarium (1998–) *FloraBase—the Western Australian Flora*. Department of Biodiversity, Conservation and Attractions. https://florabase.dpaw.wa.gov.au/ [accessed 29 April 2021]

Wilson PG, Rowe R (2004) A revision of the Indigofereae (Fabaceae) in Australia. 1. *Indigastrum* and the simple or unifoliolate species of *Indigofera*. *Telopea* 10: 651–682.

Wilson PG, Rowe R (2015) Additional taxa of *Indigofera* (Fabaceae: Indigofereae) from the Eremaean Botanical Province, Western Australia. *Nuytsia* 25: 251–284. https://florabase.dpaw.wa.gov.au/science/nuytsia/763.pdf

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Review of nomenclature for Actinidiaceae in Australia

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Keywords: Queensland, New South Wales, Victoria, systematics, taxonomy, typification

Abstract

A lectotype is chosen for Australia's only native species of Actinidiaceae, *Dillenia andreana* F.Muell. A case is made for *Saurauia andreana* (F.Muell.) Oliv. ex F.Muell. to be treated as a new combination based on *Dillenia andreana* rather than as the name of a new taxon. Notes are provided on the classification of Yang-tao (Chinese Gooseberry or Kiwifruit), *Actinidia chinensis* var. *deliciosa* (A.Chev.) A.Chev., a taxon occasionally naturalised in Australia, for use on the online *Flora of Australia*.

Introduction

A single species of native Actinidiaceae is recognised in Australia, in the genus *Saurauia* Willd. There are around 300 species of *Saurauia*, and about 50 of these are found in New Guinea, a centre of diversity for the genus (Briggs 2011) which extends to Asia and South and Central America. The Australian species, *Saurauia andreana* (F.Muell.) Oliv. ex F.Muell., is described and illustrated by Mueller (1865: 175); Bailey (1886: 7); Bailey (1899: 106, pl. V); Bailey (1913: 46, fig. 42); Cooper and Cooper (1994, pl.; 2004, pl.); Zich *et al.* (2020; figs) and Barrett (2021). There is confusion around the correct attribution of authorship of the current name for this species (see summary of early publications below) which continues today. Two names are most commonly cited in published literature and treated as if they are based on separate types, as *Dillenia andreana* F.Muell. and *Saurauia andreana* Oliv. ex F.Muell.

Ferdinand Mueller (1865: 175) first described the taxon as *Dillenia andreana* F.Muell. (Dilleniaceae) based on a collection by John Dallachy in 1860 from the Mackay River in north Queensland, with specimens sent to MEL and some of these subsequently distributed from there. Mueller indicated in the protologue that he was naming the species in honour of Édouard-François André (1840–1911), a French horticulturist and landscape architect, and sent at least one specimen to André (now held in P).

In 1884 a request was sent to Mueller for specimens of taxa he had described that were not yet present in the herbarium collections at K. William T. Thiselton-Dyer, the then-Assistant Director, indicated that a species list (now missing) had been sent to Mueller on 5 April 1884 (Kew Correspondence, Mueller 1882–1890, folio 76). The K sheet of *Dillenia andreana* was received there in July 1884 as part of a batch of specimens sent by Mueller in response. This specimen, K 000761751 (http://specimens.kew.org/herbarium/K000761751),

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appears to be the basis for Daniel Oliver (K) recognising that the taxon belonged in *Saurauia*, with the form of the handwriting in pencil 'Saurauja aff. S. altissimae' matching other annotations (presumably by Oliver, but possibly by another member of staff) on specimens at K from around this time. Someone else has added an annotation 'Saurauja andreana (F. v. Muell.) Oliv.' In October 1884 Oliver, in a memorandum 'For F. v. Mueller', wrote: "Amongst the specimens recd. [latterly] is Dillenia Andreana, F.v.M. (Fragm. Fl Austr. V. 175). This is no doubt a Saurauja & the first representative of Ternströmiaceae noted in Australia — so far as I know." (Kew Correspondence, Mueller 1882–1890, folio 113). Oliver's re-determination was presumably communicated to Mueller, who used the new genus name in a letter to J.D.Hooker (which from internal evidence was probably written on 15 December 1884) and indicated that the taxon was only known to him from one collection: "Since I had the Sauravia first, I never got any more of it, so it never came before me again..." (Kew Correspondence, Mueller 1882–1890, folio 126).

Mueller included the designation '*Sarauia Andreana* Oliver (inedited)' in the second supplement to his *Systematic Census of Australian Plants* (1885: 3). While this is the first published reference in which the designation appears, it is not a validly published name, lacking a description or diagnosis or any reference to an earlier description or diagnosis.

Saurauia andreana 'Oliv. ex F.Muell.' was validly published the following year in Bailey (1886: 7; placed in Ternstroemiaceae). The name is attributed to '*Oliver (inedited)*' The description in Bailey (1886) is essentially an English translation of Mueller's original Latin protologue for *Dillenia andreana* (Mueller 1865: 175), and there is a note immediately following that states that it was '*Kindly furnished by Baron Mueller for this work.*' However, there is no explicit reference to any previous publications.

There appear to be two erroneous statements in Bailey's (1886) work. Firstly, it states 'Hab. : Near the border of New South Wales.' but the species is restricted in distribution to north Queensland, between Cardwell and Cape Tribulation. Historically New South Wales included Queensland, but Queensland was established as a separate colony in 1859 and as Colonial Botanist from 1881 Bailey would presumably have been well aware of its boundaries. Secondly, an etymology is given (as in all of Bailey's own species descriptions in this supplement) as "After H. Andrae." [i.e. Hans Andrae, who collected for Mueller in New South Wales near the Lachlan River and Cobar during the 1870s and 1880s]. If the species were named for him the correct orthography for the epithet would presumably be *andraeana*, but that form is not used in any known works. It is unclear exactly how much of the text was supplied by Mueller and it is possible that Bailey assumed the epithet referred to H. Andrae, given his collections in Australia and association with Mueller.

Interestingly, Mueller (1889: 14) attributes the name to 'Dyer & Oliver in Bailey', with direct reference to his original description of *Dillenia andreana* as 'M.fr.V,175', but there is no mention of [Thiselton-]Dyer in Bailey (1886), nor has any other mention been found in other publications.

Bailey (1899: 106) provides some more details, stating that the name was attributed to Oliver '(inedited)' by Mueller 'in letter', and specifically cites *Dillenia andreana* as a synonym. The distribution is given as "Hab.: Freshwater Creek near Cairns and creeks about Bellenden Ker..." [i.e. north Queensland] and the etymology is also corrected to "After E. André". Correspondence between Mueller and Bailey for this period has not been found so the source of these corrections is unknown. Bailey (1913: 46) later simply attributes the name to Oliver, but includes a full reference to the basionym *Dillenia andreana* F.Muell.

Domin (1928) lists '*Saurauja Andreana* Oliv ex F. M. Bail.' and lists an additional name in synonymy. Domin attributes the latter name, *Synarrhena andreana*, to "F. v. MUELL. Fragm. V. 175 (1866) in syn." [i.e. F.J.H. von Mueller, *Fragm.* 5(39): 175 (1866)]. While Mueller (1866) provisionally suggests that *Dillenia andreana* F.Muell. may represent the type of a new genus, *Synarrhena*, he does not validly publish the names at genus or species ranks.

If we accept that there is no basionym cited by Bailey (1886: 7), the conditions for publication of *Saurauia andreana* as the name of a new taxon are fulfilled, and ICN Art. 41.4 (Turland *et al.* 2018) is then relevant. In this case, one can interpret the fact that Mueller adopted the genus name supplied by Oliver and re-used his previous epithet (the only known case where he named a taxon in honour of André) as indicating a 'presumed intention' to provide a new combination based on *D. andreana*.

There is no specific mention of Mueller's publication or earlier name in Bailey (1886: 7), but the similarities of the description, and its attribution to Mueller, could alternatively be considered to constitute an indirect reference to the basionym *Dillenia andreana* F.Muell. (ICN Art. 38.14 and Art. 41.3; Turland *et al.* 2018). This presents a second option that leads to the same conclusion.

If *Saurauia andreana* were treated as the name of a new taxon, the authorship would be 'Oliv. ex F.Muell.' and any selection of a lectotype would have to be made in the context of Bailey's (1886) publication. It is likely

however that suitable original material does not exist, given Mueller's statement that he had received specimens of the taxon only once prior to 1885 and the cited habitat "Near the border of New South Wales". However, if either a presumed intent to make a new combination (Art 41.4), or an indirect reference is accepted here (Art. 41.3), then a lectotype is only needed for *Dillenia andreana* F.Muell., and the correct citation in *Saurauia* is *S. andreana* (F.Muell.) Oliv. ex F.Muell.

We consider there to be sufficient reasons to accept *Saurauia andreana* as a new combination, and below select a lectotype for the basionym, *Dillenia andreana*.

Saurauia Willd., *Der gesellschaft naturforschenden freunde zu Berlin, Neue schriften* 3: 407, t. 4 (1801), *orth. cons. Type*: *Saurauia excelsa* Willd.

Saurauia andreana (F.Muell.) Oliv. ex F.Muell. in F.M. Bailey, *A synopsis of the Queensland flora. Supplement* 1: 7 (1886), (as *Saurauja Andreana*).

Basionym: *Dillenia andreana* F.Muell., *Fragmenta phytographiae Australiae* 5(39): 175 (1865).

Type citation: 'Ad ripas fluminis Mackay-River, Dallachy.'

Type: Queensland: Banks of the Mackay River [Tully River, Rockingham Bay], 11 Aug. 1860, *J. Dallachy s.n.* (lecto (here designated): MEL 2283107; isolecto: MEL 2283108; K 000761751; P 00682291 [ex Herb. E.André], images seen for all).

Synarrhena andreana Domin, *Bibliotheca Botanica* 22(89): 979 (1928), *nom. inval., pro syn.*

Typification: Four sheets have been located that all appear to be duplicates of the original collection, though each has slightly differing label information. Two sheets in MEL represent the best material on which to base the name, and MEL 2283107 is selected as the lectotype as it has a slip with the original collection notes and a separate label with the name *Dillenia andreana* in Mueller's hand. The second sheet (MEL 2283108) has the same information duplicated in a different hand on a single label. Two other sheets (at K and P) are simply labelled 'Rockingham Bay', with no collector or date, but both have labels from Mueller's herbarium with the name *Dillenia andreana*. It is considered reasonable to assume both are duplicates and therefore isolectotypes.

A kiwifruit by any other name

Kiwifruit is cultivated in a number of locations in Australia and is occasionally naturalised in Queensland, New South Wales and Victoria (Messina 2015). Deciding on the most appropriate taxonomic rank for the commercially popular Kiwifruit (Yang-tao or Chinese Gooseberry) has been much debated (Li *et al.* 2007a, 2007b, 2010; Huang 2014). The options are inclusion under a broad concept of *Actinidia chinensis* Planch., or recognition either as a distinct variety, *A. chinensis* var. *deliciosa* (A.Chev.) A.Chev., or as a distinct species, *A. deliciosa* (A.Chev.) C.F.Liang & A.R.Ferguson.

Reticulation as a result of hybridisation is common in the genus *Actinidia* Lindl., and it has been suggested that kiwifruit (a polyploid taxon, 6x) may be a hybrid between *A. chinensis* var. *chinensis* (2x or 4x) and another taxon whose identity was uncertain (Chat *et al.* 2004). A very detailed study by Liu *et al.* (2017) utilising whole-genome data for 40 *Actinidia* samples has shown complex patterns of reticulation in the genus, reflecting both old and recent hybridisation events. An interesting pattern emerged showing significant and widespread reticulation between *A. chinensis* var. *chinensis* and numerous related species and varieties, but relatively little reticulation involving *A. chinensis* var. *deliciosa*. Analysis of nuclear genomic data showed that these two varieties are very closely related, but the total evidence analyses suggest that *A. chinensis* var. *deliciosa* has remained relatively isolated from the remainder of the *A. chinensis* complex, and the change to 6x may be a relatively effective barrier against hybridisation relative to 4x and 2x relatives (Liu *et al.* 2017). Some reticulation in *A. chinensis* var. *deliciosa* was identified (cytonuclear conflicts), linking the genome of var. *deliciosa* to the chloroplast genomes of *A. callosa* var. *strigillosa* C.F.Liang and *A. zhejiangensis* C.F.Liang and to the mitochondrial genome of *A. arguta* var. *giraldii* (Diels) Vorosch. (Liu *et al.* 2017: see figs 1 and S13).

Given that the genetic history of *Actinidia chinensis* var. *deliciosa* is supported as distinct from var. *chinensis*, the recognition of the variety for taxonomic purposes in Australia is recommended. Currently only the species, *A. chinensis*, is listed as an accepted name by the Australian Plant Census (https://biodiversity.org.au/nsl/services/search/taxonomy; accessed May 2021).

Actinidia chinensis var. ***deliciosa*** (A.Chev.) A.Chev., *Revue de Botanique Appliquee et d'Agriculture Tropicale* 21: 241, t. 1 (1941). *Actinidia latifolia* var. *deliciosa* A.Chev., *Revue de Botanique Appliquee et d'Agriculture Tropicale* 20(221): 12, t. 1, 2 (1940). *Actinidia deliciosa* (A.Chev.) C.F.Liang & A.R.Ferguson, *Guihaia* 4(3): 181 (1984).

Type: published illustration: "Fructification du meme," Planche II in Chevalier, (1940), (lectotype); China: Hubei: Wufeng, 2 Aug. 1959, *R.H. Huang 1991* (epitype: HIB), both lectotype and epitype designated by Li *et al.*, *Novon* 20(1): 58 (2010).

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References

Bailey FM (1886) *A synopsis of the Queensland flora; containing both the phaenogamous and cryptogamous plants. First Supplement*. (James C. Beal, Government Printer: Brisbane) https://books.google.com.au/books/download/A_Synopsis_of_the_Queensland_Flora.pdf?id=WgUmAQAAMAAJ&output=pdf&sig=ACfU3U3kNgCvQN_OCURq4DQbb3wifpuORg

Bailey FM (1899) *The Queensland flora. Part 1. Ranunculaceae to Anacardiaceae*. (H.J. Diddams and Co.: Brisbane) https://www.biodiversitylibrary.org/item/115021#page/158/mode/1up

Bailey FM (1913) *Comprehensive catalogue of Queensland plants both indigenous and naturalised.* (A.J. Cumming, Government Printer: Brisbane) https://www.biodiversitylibrary.org/item/123358#page/66/mode/1up

Barrett RL (2021) *Saurauia andreana*. In: P.G.Kodela (ed.) Actinidiaceae. In: *Flora of Australia* (electronic resource). (Australian Biological Resources Study, Department of Agriculture, Water and the Environment: Canberra) https://profiles.ala.org.au/opus/foa/profile/Saurauia%20andreana [Published online 13 May 2021]

Briggs M (2011) *Saurauia* (Actinidiaceae) of New Guinea: current status, future plans. Gardens' Bulletin Singapore 63: 77–82. https://www.biodiversitylibrary.org/page/43627000#page/87/mode/1up

Chat J, Jáuregui B, Petit RJ, Nadot S (2004) Reticulate evolution in kiwifruit (*Actinidia*, Actinidiaceae) identified by comparing their maternal and paternal phylogenies. *American Journal of Botany* 91: 736–747. https://doi.org/10.3732/ajb.91.5.736

Chevalier A (1940) Sur des lianes fruitières intéressantes : Les *Actinidia*. Journal d'agriculture traditionnelle et de botanique appliquée 20: 10–15. https://www.persee.fr/doc/jatba_0370-3681_1940_num_20_221_6060

Cooper W, Cooper WT (1994). *Fruits of the Rainforest.* (GEO Productions: Chatswood)

Cooper W, Cooper WT (2004) *Fruits of the Australian Tropical Rainforest.* (Nokomis Editions: Melbourne)

Domin K (1928) Beitrage zur Flora und Pflanzengeographie Australiens. *Bibliotheca Botanica* 22(89). (E. Schweizerbart, Stuttgart)

Huang H (2014) *The genus* Actinidia, *a world monograph*. (Beijing, China: Science Press)

Kew Correspondence: Australia, Mueller (1882–1890), Archives, Royal Botanic Gardens, Kew [Annotated transcriptions accessed courtesy of Mueller Correspondence Project, Royal Botanic Gardens Melbourne]

Li JQ, Li XW, Soejarto DD (2007a) A revision of the genus *Actinidia* from China. *Acta Horticulturae* 753: 41–44.

Li JQ, Li XW, Soejarto DD (2007b) Actinidiaceae. In: Wu ZY, Raven PH, Hong DY (eds), *Flora of China*. *Volume 12*. (*Hippocastanaceae through Theaceae*). pp. 334–360. (Science Press: Beijing, and Missouri Botanical Garden Press: St. Louis). http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=250076893

Li X-W, Shi, Q-F, Li J-Q (2010) Lectotypification of *Actinidia latifolia* var. *deliciosa* (Actinidiaceae). *Novon* 20: 57–59. https://doi.org/10.3417/2008042

Liu Y, Li D, Zhang Q, Song C, Zhong C, Zhang X, Wang Y, Yao X, Wang Z, Zeng S, Wang Y, Guo Y, Wang S, Li X, Li L, Liu C, McCann HC, He W, Niu Y, Chen M, Du L, Gong J, Datson PM, Hilario E, Huang H (2017) Rapid radiations of both kiwifruit hybrid lineages and their parents shed light on a two-layer mode of species diversification. New Phytologist 215: 877–890. https://doi.org/10.1111/nph.14607

Messina A (2015) Actinidiaceae. In *VicFlora - Flora of Victoria*. https://vicflora.rbg.vic.gov.au/flora [accessed May 2021]

Mueller, F.J.H. (1875) *Fragmenta phytographiae Australiae. Volume V*. (Government Printer, Melbourne) https://www.biodiversitylibrary.org/item/7222#page/184/mode/1up

Mueller, F.J.H. von (1885) *Systematic census of Australian plants, with chronologic, literary and geographic annotations: second annual supplement (for 1884).* (Government Printer, Melbourne)

Mueller, F.J.H. von (1889) *Second systematic census of Australian plants, with chronologic, literary and geographic annotations.* (Government Printer, Melbourne) https://www.biodiversitylibrary.org/page/19503336#page/24/mode/1up

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF (2018) (Eds) *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159.* (Koeltz Botanical Books: Glashutten) https://doi.org/10.12705/Code.2018

Zich FA, Hyland BPM, Whiffin T, Kerrigan RA (2020) *Australian Tropical Rainforest Plants* (Edn 8). https://apps.lucidcentral.org/rainforest/ [accessed May 2021]

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Hornworts of Australia: three new *Anthoceros* L. (Anthocerotaceae) species from New South Wales

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Abstract

Three new species of *Anthoceros* sect. *Fusiformes* Grolle are described, all occurring on the North West Slopes and Plains of New South Wales and all sharing spore characteristics of a smooth unornamented strip on either side of the triradiate mark on the proximal face. Illustrations and a distribution map are provided for the three new species, *Anthoceros apocynon* Cargill & Palsson, *A. palssoniae* Cargill and *Anthoceros wellmanii* Cargill, along with a key to Australian Anthocerotaceae.

Introduction

Populations of *Anthoceros* L. *sens. str.* in Australia are not common. The genus is defined by the presence of gametophyte internal schizogenous cavities (Fig. 1B), tiered jacket cells of the antheridia (Fig 1C, E), darkly coloured spores, and thin-walled multicellular pseudoelaters (Fig. 1D). Often, in the field it can be identified by the frilly appearance of the thallus due to numerous rows of lamellae over the dorsal surface (Fig. 1A). The most common species in Australia is *Anthoceros punctatus* L. though recent molecular data has confirmed that *A. agrestis* Paton is also present on the continent (Dawes *et al.* 2020). Both species belong to *Anthoceros* sect. *Anthoceros* (Grolle 1976) [= '*punctatus*-group' of Proskauer (1958)] defined by their dimorphic spore distal and proximal patterns. The spore distal face of section *Anthoceros* is spiny and the proximal face foveate with smooth or spiny borders around the fovea. Spores of *Anthoceros* sect. *Fusiformes* Grolle (Grolle 1976) [= '*fusiformis*-group' of Proskauer (1958)] are also dimorphic but the proximal face is defined by a distinct smooth strip either side of the triradiate mark.

McCarthy (2006) listed 14 species of *Anthoceros* but of those, ten species are now placed in other genera of the Anthocerotaceae or are regarded as synonymous with other species in the genus. While the genus in the strictest sense still requires a comprehensive revision for Australia, recent collections of hornworts from the North West Slopes of New South Wales revealed three unusual species. All three species bear spores with a smooth unornamented strip on either side of the triradiate mark of the proximal face, placing them in sect. *Fusiformes*. Species exhibiting this spore pattern have not previously been described for Australia and these collections represent three new species.

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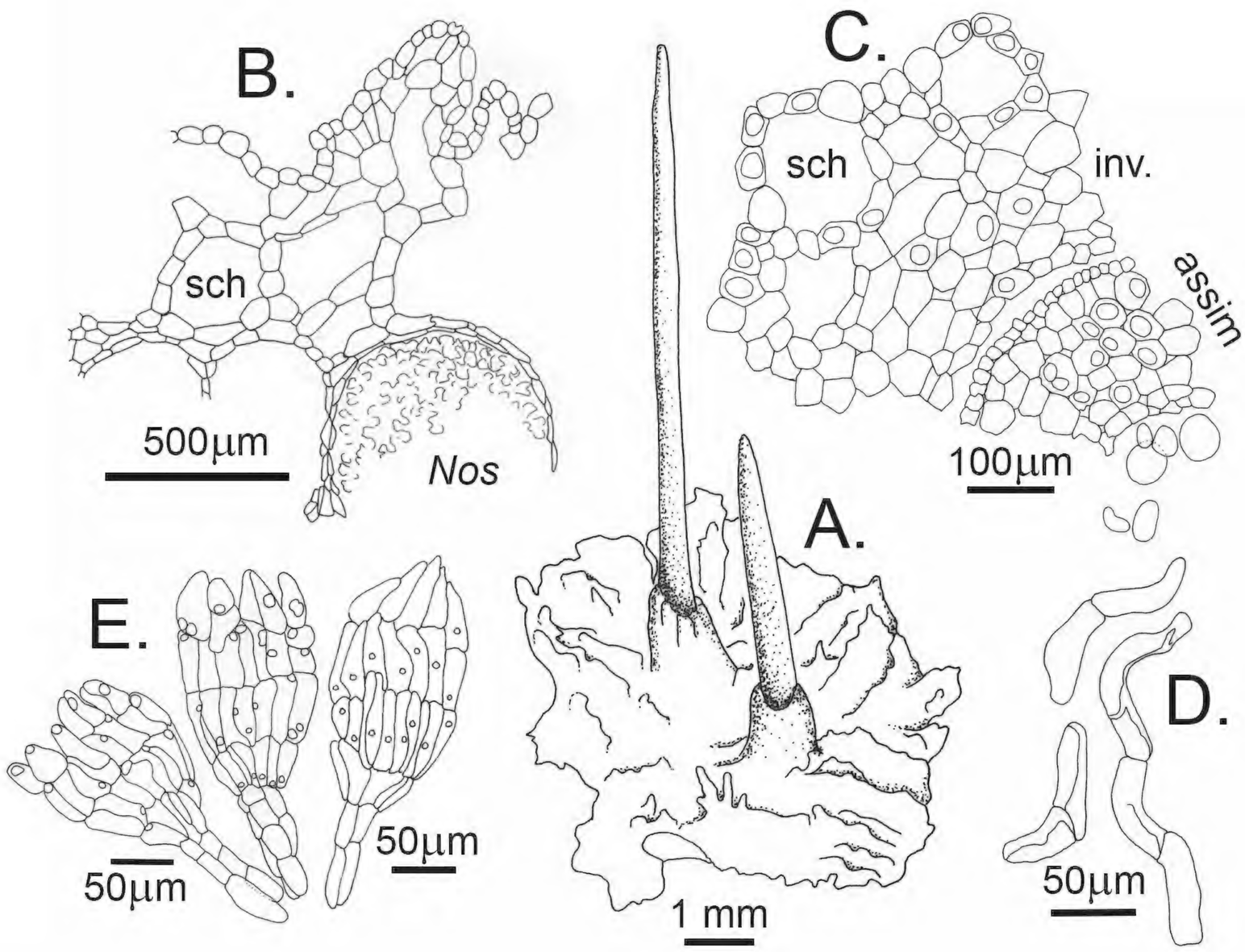

Figure 1. Characteristics of the family. A. Fertile plant with dorsal lamellae giving the plant a 'frilly' appearance. B. Transverse section through thallus showing schizogenous cavities (sch) throughout (*Nos* = *Nostoc* colony). C. Transverse section through involucre and sporogone showing schizogenous cavities (sch) in involucre (inv.) (assim = assimilative tissue). D. Pseudoelaters. E. Tiered jacket cells of the antheridia. All drawings by D.C. Cargill.

Two out of the three species were collected following a number of years of drought in western New South Wales which was broken by rains during a La Niña weather pattern year in Australia in 2020. This weather event led to significant germination of bryophyte spores and tubers, not only hornworts but also many *Riccia* L. and *Fossombronia* Raddi species (D.C. Cargill pers. obs.). The species described here are apparently confined to dryer areas of eastern Australia, regions where bryologists typically do not collect, particularly in very dry years, and hence no previous collections of these taxa have been made.

Key to Australian species of Anthocerotaceae

1. Plants pale green to olive-green; short irregular lamellae growing perpendicular to dorsal surface, giving plants a 'frilly' appearance, plants prostrate or erect 2

1. Plants green to olive-green; dorsal surface smooth, plants not appearing 'frilly'; plants always prostrate..... 6

2. Sporophytes long (up to 80 mm long) and thin; spores spinose on the distal face, punctate on the proximal face only ..... **Anthoceros punctatus**

2. Sporophytes short (2.4–10.8 mm long) and thick; spores with or without spines on distal face; never punctate on the proximal face 3

3. Thallus in rosettes or half-rosettes if prostrate, or conical if erect, spores smooth distally ..... **Anthoceros palssoniae**

3. Thallus in rosettes or half rosettes, prostrate; spores spiny on distal face..... 4

4. Spores spiny on both distal and proximal faces 6

4. Spores spiny on distal face only, with smooth strip on either side of trilete mark; proximal face with compressed vermiculate like ridges and projections 5

5. Spores with numerous short spines (15–20 across the diameter) ..... **Anthoceros apocynon**

5. Spores with fewer, larger spines (8–10 across the diameter) ..... **Anthoceros wellmanii**

6. Plants broadly fan-shaped, not pinnately lobed 7

6. Plants strap-shaped, ±pinnately lobed ..... **Folioceros fuciformis**

7. Spores tetrahedral; medium, 40–55 μm in diameter, all spores normal; pseudoelaters short 72.5–143 μm long, no thickenings ..... **Anthoceros fragilis**

7. Spores apolar; large, 64–82μm in diameter, mixed with aborted or immature spores; pseudoelaters short 22–170 μm long, occasionally with irregular thickening bands ..... **Anthoceros capricornii**

Descriptions of new taxa

Anthoceros apocynon Cargill & Palsson, ***sp. nov.***

Diagnostic characters: Similar to *Anthoceros palssoniae* and *A. wellmanii* with which it shares short, thick sporophytes and the presence of lamellae on the dorsal surface of the gametophyte thallus, but differs in spore patterning. *Anthoceros apocynon* spores are distally spiny (vs smooth distal face in *A. palssoniae*) and there are numerous, finer spines on the distal face (vs fewer and larger spines in *A. wellmanii*).

Type: AUSTRALIA. New South Wales. North West Slopes. Pilliga State Conservation Area (SCA), Dog Proof Fence Rd, in tributary of Goona Ck, edge of creekline in plain of *Allocasuarina luehmannii* – ironbark woodland, 13 Sept. 2020 *R.L.Palsson & K.D.Durham 398(3)pp* (holotype: CANB 923469; isotype: NSW).

?Dioicous or strongly protandrous. Plants in patches of rosettes or half rosettes; unbranched or 2 or 3 branches forming ± fan-shaped plants, growing prostrate; 2.9–4.5 mm long, 3.0–4.75 mm wide, lobes 0.1–0.9 mm wide, margins highly dissected into smaller lobes; live plants not seen, plants becoming dark blackish green when dry. Thallus cavernous, ecostate, mid-thallus two to three mucilaginous cavity layers thick, plano-convex to fusiform in transverse section. Dorsal surface with many short lamellae and lobes. Dorsal epidermal cells polygonal, quadrate to hexagonal, isodiametric towards the apex, becoming elongate-rectangular basally, 65–150 × 30–62.5 μm, internal cells not measured; a single chloroplast per cell, pyrenoid absent , starch-free zone present. Ventral clefts not observed. Ventral epidermal cells polygonal, quadrate to hexagonal, isodiametric towards the apex becoming elongate-rectangular basally, 65–150 × 30–62.5 μm, a single chloroplast per cell, pyrenoid absent, starch-free zone present. *Nostoc* colonies present, few, scattered through thallus, appearing as large dark olive-green globose colonies. Rhizoids ventral, hyaline to pale brown, empty or mainly granular. Specialised asexual reproduction absent. Androecium not seen. Involucre erect, turbinate, 0.8–1.45 mm long, 3–5 cell layers thick or reduced to a compressed thin layer at maturity. Capsule thickly conical, emergent, 2.35–6.8 mm long, bearing two valves, opening only on one side, remaining straight and not twisted upon drying, becoming dark brown to black with maturity, foot not observed. Capsule assimilative layer 3–5 cells thick (95–190 μm thick) and sporogenous layer 1 tetrad layer thick, with well-developed columella occupying from 3/4 to full length of capsule, number of cells making up columella not observed, pseudoelaters frequently remaining attached. Epidermal cells of capsule elongate-rectangular, 50–137.5 × 12.5–25 μm, walls very thick, stomata present, 42.5–60 × 35–50 μm. Spores dark brown to almost black, irregularly globose to triangular-globose in polar view, tetrahedral shape in equatorial view, concave at centre of proximal surface apex due to flanges on either side of triradiate mark, equatorial diameter 67.5–85 μm, polar height 42.5–57.5 μm. Distal face covered with short clavate-shaped spines coalescing to form short ridges, spiny around the circumference; cingulum absent; proximal face with a flange on either side of the triradiate mark, narrow, wavy subtending a smooth strip either side of the triradiate mark; triradiate mark thin, but distinct. Pseudoelaters translucent brown, remaining attached or becoming detached from columella, thin-walled; 1–4 cells long, 32.5–87.5 μm long, 15–37.5 μm wide; frequently branched, surface smooth. Figs 2–7.

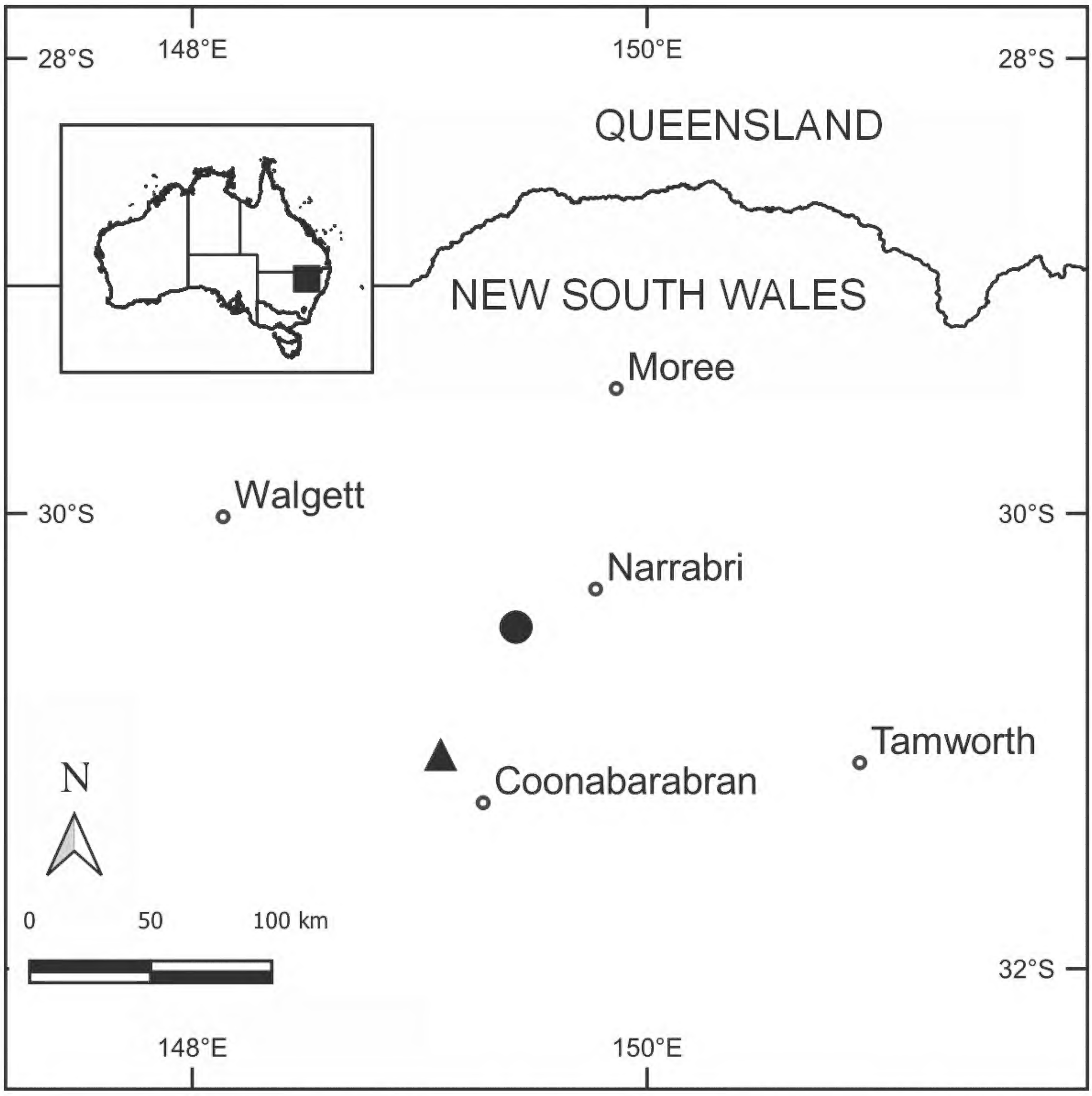

Figure 2. Distribution of *Anthoceros apocynon* and *A. palssoniae* (●) *A. wellmanii* (▲).

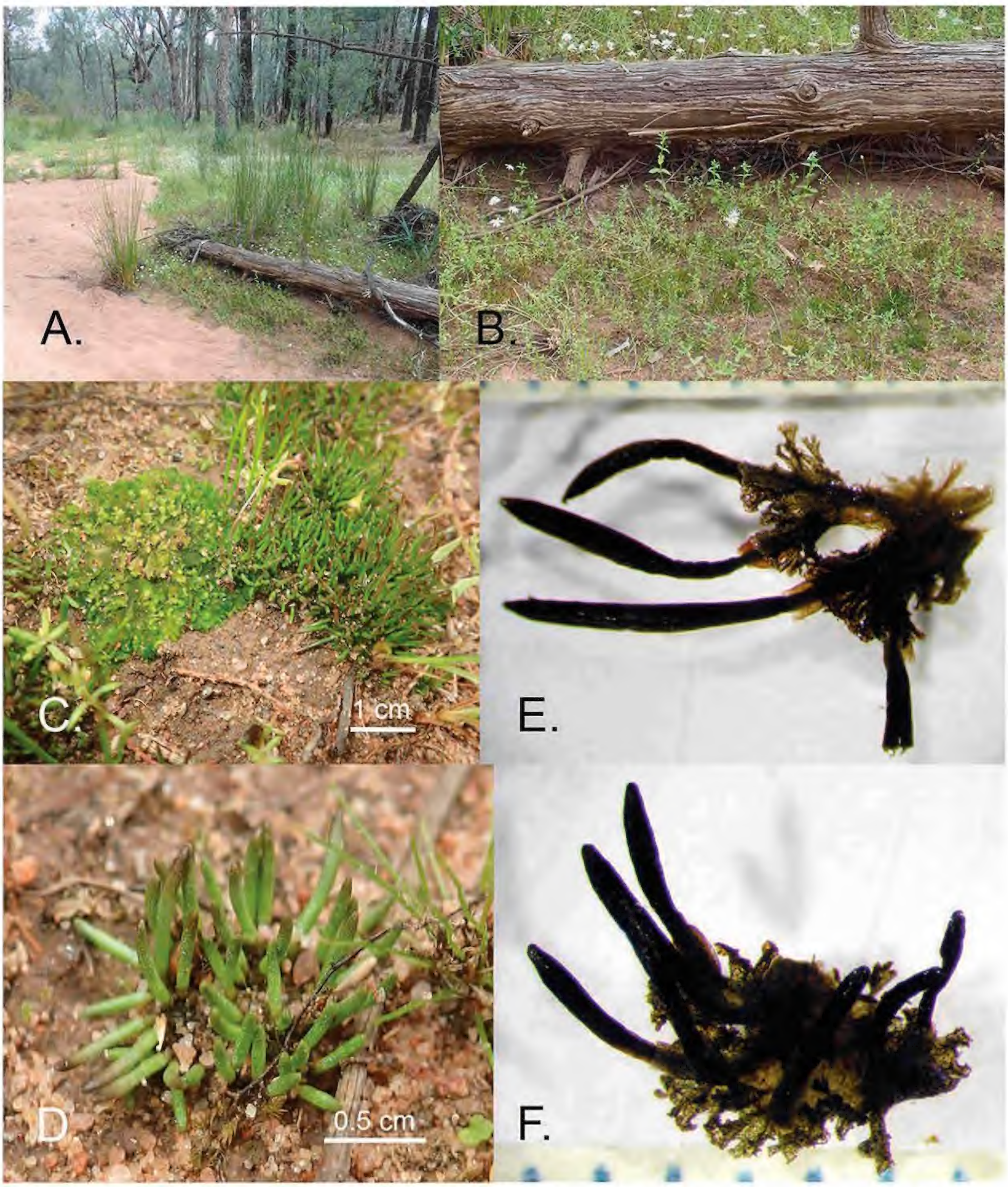

Figure 3. A, B. Habitat of *Anthoceros apocynon* and *A. palssoniae*. C. *Anthoceros apocynon* (on the right next to a rosette of *Phaeoceros* sp.) in situ (from *R.Palsson 398(2)* CANB). D. Fertile plants of *A. apocynon* in their natural habitat (from *R.Palsson 398(3)* CANB). E, F. Individual plants of *A. apocynon*, scale divisions = 1 mm (from *R.Palsson 398(3)* CANB). Photos A–D by R. Palsson; photos E–F by D.C. Cargill.

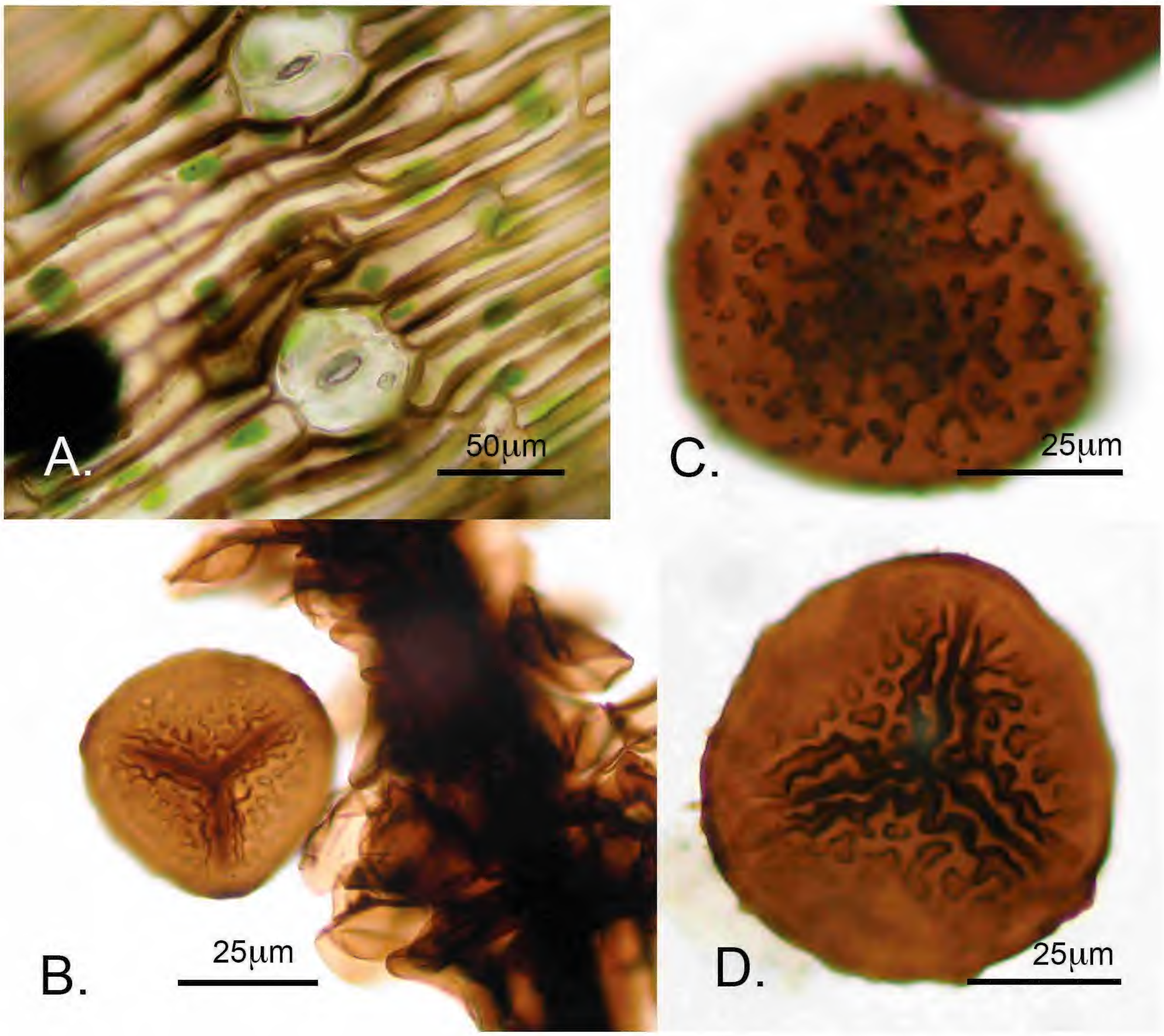

Figure 4. *Anthoceros apocynon*. A. Light micrographs (LM) of epidermal cells of the sporophyte. B. LM of columella with pseudoelaters attached and proximal view of spore to the left. C. LM of distal view of spore. D. LM of proximal view of spore. (All images from *R.Palsson 398(3)* CANB). Photos by D.C. Cargill.

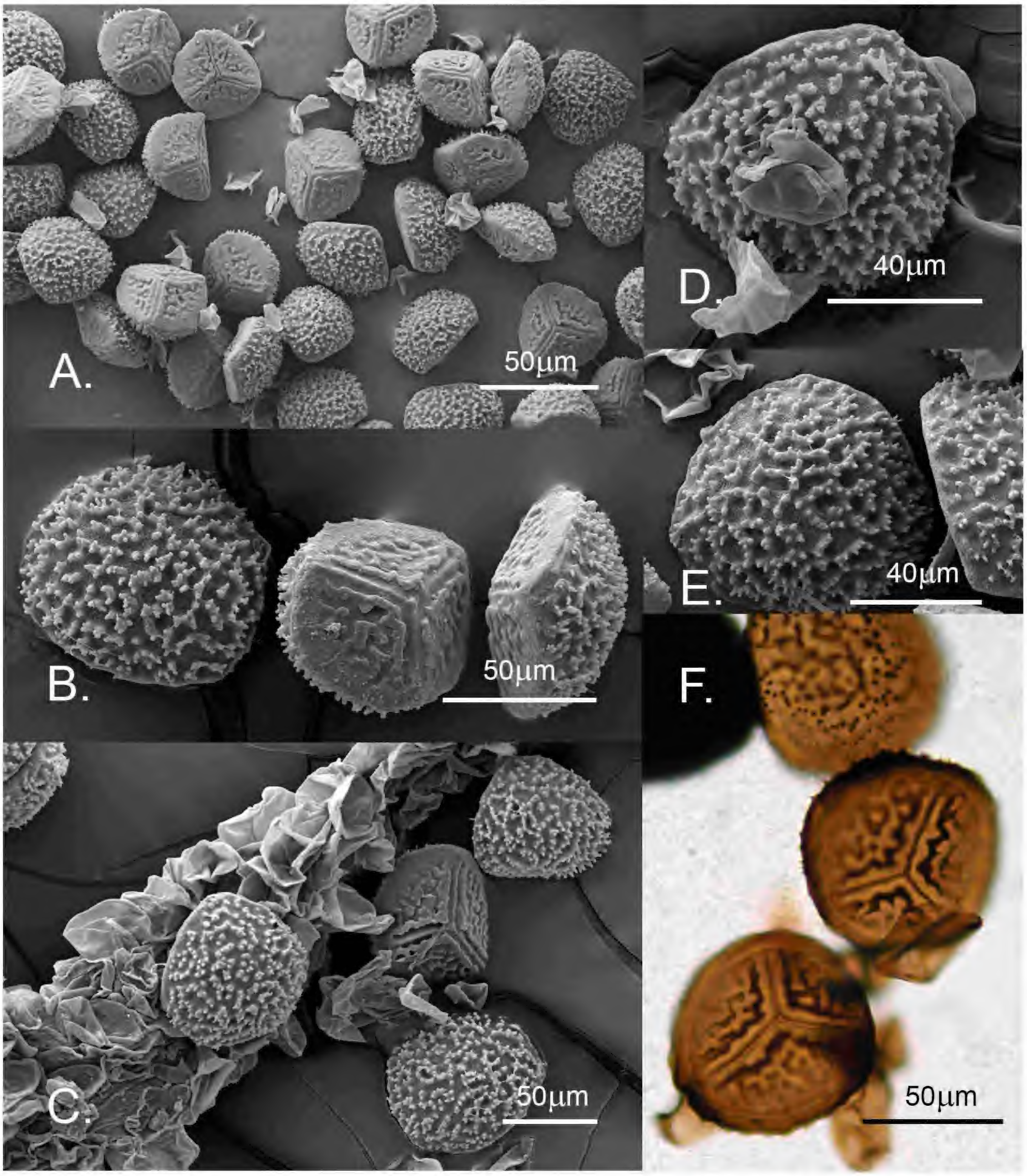

Figure 5. SEM and LM images of spores of *Anthoceros apocynon*. A, B, D, E. Showing different faces of spores: distal, proximal and side views. C. Columella of sporophyte with spores and pseudoelaters attached. F. LM view of spores showing both distal and proximal faces. (All images from *R.Palsson 398(3)* CANB). Photos by D.C. Cargill.

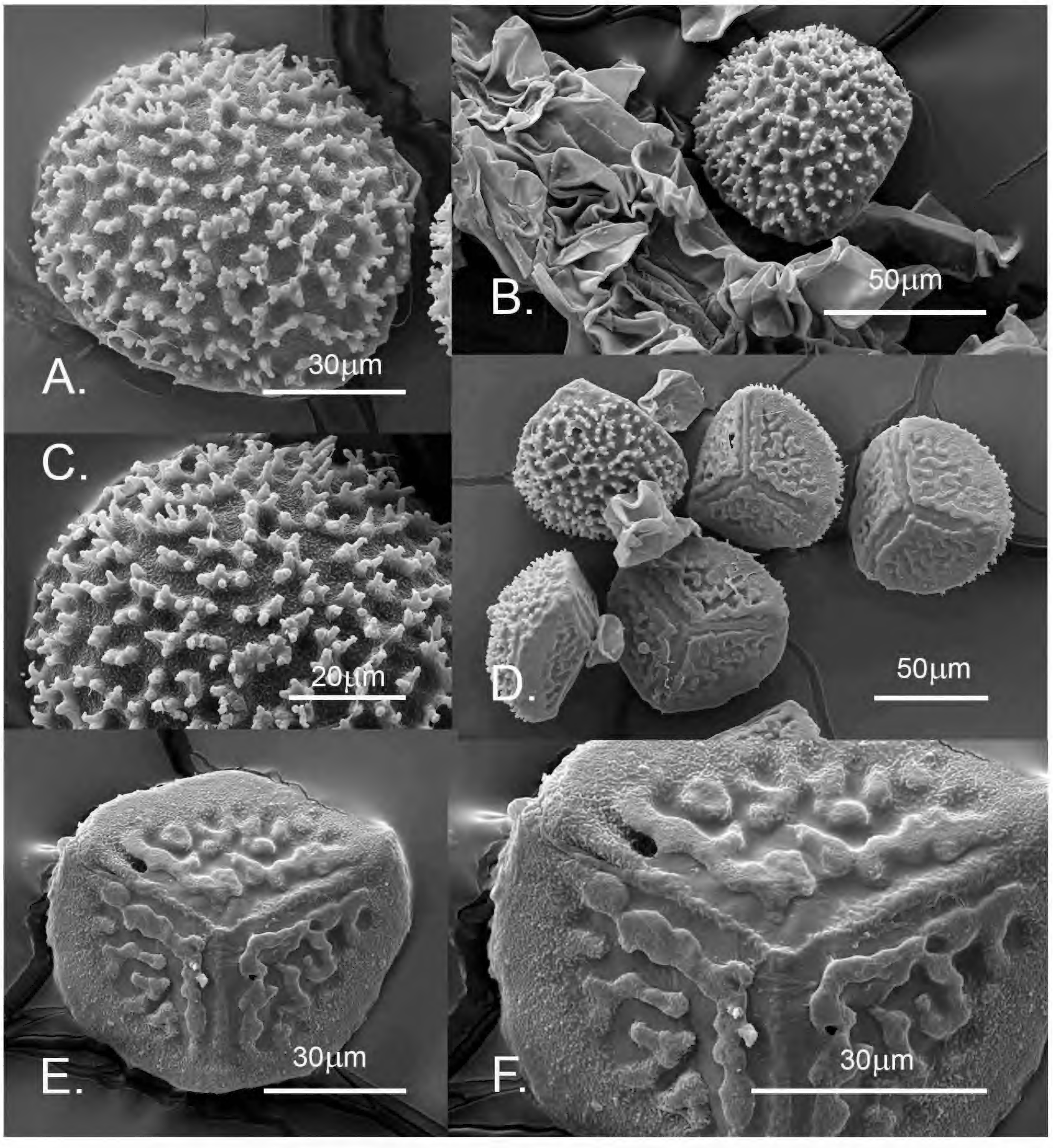

Figure 6. A–F. SEM images of spores of *Anthoceros apocynon* showing variations in the distal and proximal patterns. (All images from *R.Palsson 398(3)* CANB). Photos by D.C. Cargill.

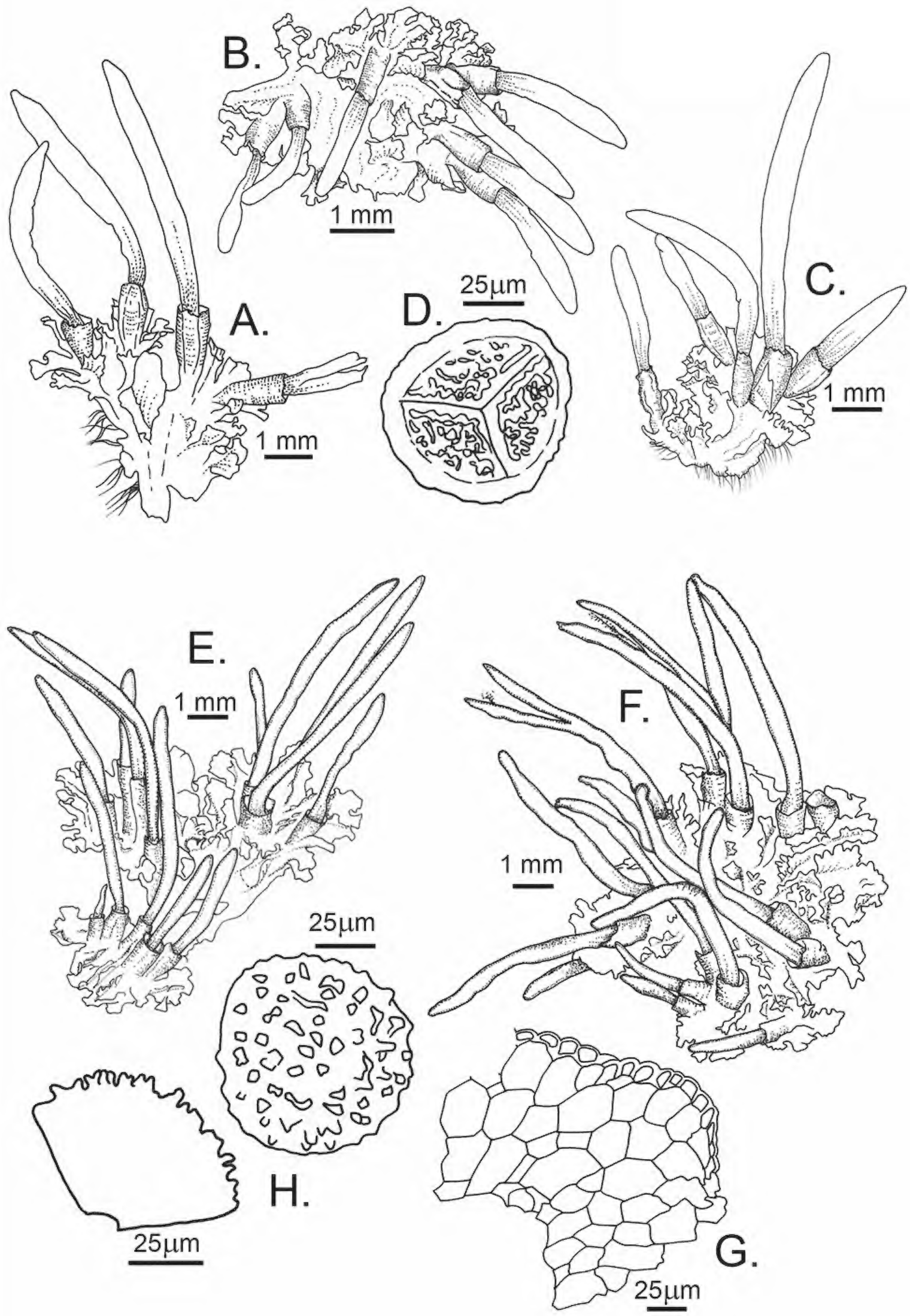

Figure 7. A–C. Whole plants of *Anthoceros apocynon*. D. Proximal view of spore of *A. apocynon*. (All drawings from *R.Palsson 398(3)* CANB). E, F. Whole fertile plants of *Anthoceros wellmanii*. G. Cross-section through the sporophyte of *A. wellmanii*, showing the single layer of epidermal cells and the 5-celled assimilative layer below that. H. Distal view and side view of spores of *A. wellmanii*. (All drawings from *P.Wellman 588A.1* CANB). Drawings by D.C. Cargill.

Notes. The spores of this species bear a smooth strip either side of the triradiate mark, placing it in sect. *Fusiformes*. The proximal flange and the ornamentation within each of the facets consist of wide, flat, hamulate muri which run into a broad ring around the proximal face with a micro-ornamentation of tiny papillae and baculae (Fig 5E, F). The distal face is covered in numerous clavate spines which occur in short rows of two or more spines coalescing into ridges. The micro-ornamentation on the face of the distal surface consists of numerous baculae (Figs 4, 5A, B, C). Also, pseudoelaters are uncharacteristically short, a phenomenon of species with large spores (Figs 4A, C, D and 5B, D) (Villarreal *pers. comm*. 13th Oct. 2020; see *A. adscendens*, *A. capricornii*).

Vegetatively *A. apocynon* is very similar to the other two new species in the frilly nature of the thallus due to dorsal lamellae, however, plants grow prostrate rather than erect, as seen in *A. palssoniae*. The chloroplasts

of the species epidermal cells lack a pyrenoid instead showing a 'starch-free zone' (Villarreal *pers. comm.*) or 'pseudopyrenoid' a term coined by Vaughn *et al.* (1992).

Etymology. From Greek, ἀπόκῠνον, dog's bane, a noun in apposition. The epithet is in reference to Dog Proof Fence Road, adjacent to the collection locality of the type material.

Distribution and habitat. Known only from the type locality in the Pilliga State Conservation Area on the north-western slopes of New South Wales. The type collection was made from *Allocasuarina luehmannii* – ironbark woodland on a fine layer of silt over pink-brown sand. Growing with other hornworts including *Anthoceros punctatus*, *A. palssonii* and *Phaeoceros* sp.

Conservation status. This species has not been formally evaluated. A conservation coding of "Not Evaluated" (IUCN 2019) is therefore appropriate.

Anthoceros palssoniae Cargill, ***sp. nov.***

Diagnostic characters: Similar to *Anthoceros apocynon* and *A. wellmanii*, with which it shares numerous short lamellae on the gametophyte dorsal surface and short thick sporophytes, but differing in spore patterning, the spores of *A. palssoniae* are smooth distally, whereas spores are distinctly spiny distally in both *A. apocynon* and *A. wellmanii*.

Type: AUSTRALIA. New South Wales: North West Slopes. Pilliga State Conservation Area (SCA), Dog Proof Fence Rd, in tributary of Goona Ck, edge of creekline in plain of *Allocasuarina luehmannii* - ironbark woodland, 13 Sept. 2020 *R.L.Palsson & K.D.Durham 398(2)* (holotype: CANB 923468; isotype: NSW).

?Dioicous or strongly protandrous. Plants in patches of rosettes or half rosettes.. Multiple basal branching pattern to form fans of plants or single funnel-shaped plants, growing erect; 2.0–6.0 mm long, 3.4–9.0 mm wide, lobes 0.1–1.35 mm wide, margins dissected into smaller lobes; plants bright green (RHS 144A (yellow-green group) becoming dark greenish black when dry. Thallus cavernous, ecostate, mid-thallus two mucilaginous cavity layers thick, plano-convex to concave-convex to terete-shaped in transverse section. Dorsal surface with many short lamellae and ridges. Dorsal epidermal cells polygonal, quadrate to septagonal, isodiametric towards the apex, becoming elongate-rectangular basally, 40–245 × 25–57.5 μm, internal cells 62.5–345 × 22.5–125 μm, a single chloroplast per cell, pyrenoid absent, starch-free zone present. Ventral clefts not observed. Ventral epidermal cells polygonal, quadrate to octagonal, isodiametric towards the apex becoming long, thin and elongate-rectangular basally, 32.5–272.5 × 12.5–67.5 μm, a single chloroplast per cell, pyrenoid absent, starch-free zone present. *Nostoc* colonies present, few, scattered through thallus, appearing as large dark olive-green globose dots. Rhizoids ventral, hyaline to pale brown, empty or mainly granular. Specialised asexual reproduction absent. Androecium not seen. Involucre erect, cylindrical, 0.55–1.2 mm long, one layer of mucilaginous cavities and from 4–6 cell layers thick. Capsule thickly conical, emergent, 4.0–10.8 mm long, bearing two valves, frequently opening only on one side, remaining straight not twisted upon drying, becoming dark brown to black with maturity, foot bulbous. Capsule assimilative layer 4–5 cells thick (112.5–350 μm thick) and sporogenous layer 1 tetrad layer thick, with well-developed columella 16–20 cells, pseudoelaters frequently remaining attached. Epidermal cells of capsule elongate-rectangular, 47.5–150 × 12.5–27.5 μm, walls very thick, stomata present, 45–65 × 32.5–52.5 μm. Spores dark brown to almost black, irregularly globose in polar view, tetrahedral shape in equatorial view concave at centre of proximal surface apex due to flanges on either side of triradiate mark, equatorial diameter 65–80 μm, polar height 42.5–55 μm. Distal face smooth, micro-ornamentation finely papillate, shallowly crenulate around the circumference; cingulum absent; proximal face dominated by a flange on either side of the triradiate mark, margin quite wavy when mature and protrudes out from the proximal surface; the area between the flange and the triradiate mark is smooth without any ornamentation, triradiate mark thin, very distinct. Pseudoelaters translucent brown, detached or remaining attached to columella, thin-walled; from 1–5 cells long, 30–107.5 μm long, 20–40 μm wide, frequently branched, sometimes several branches per pseudoelater, surface smooth. Figs 2, 8–12.

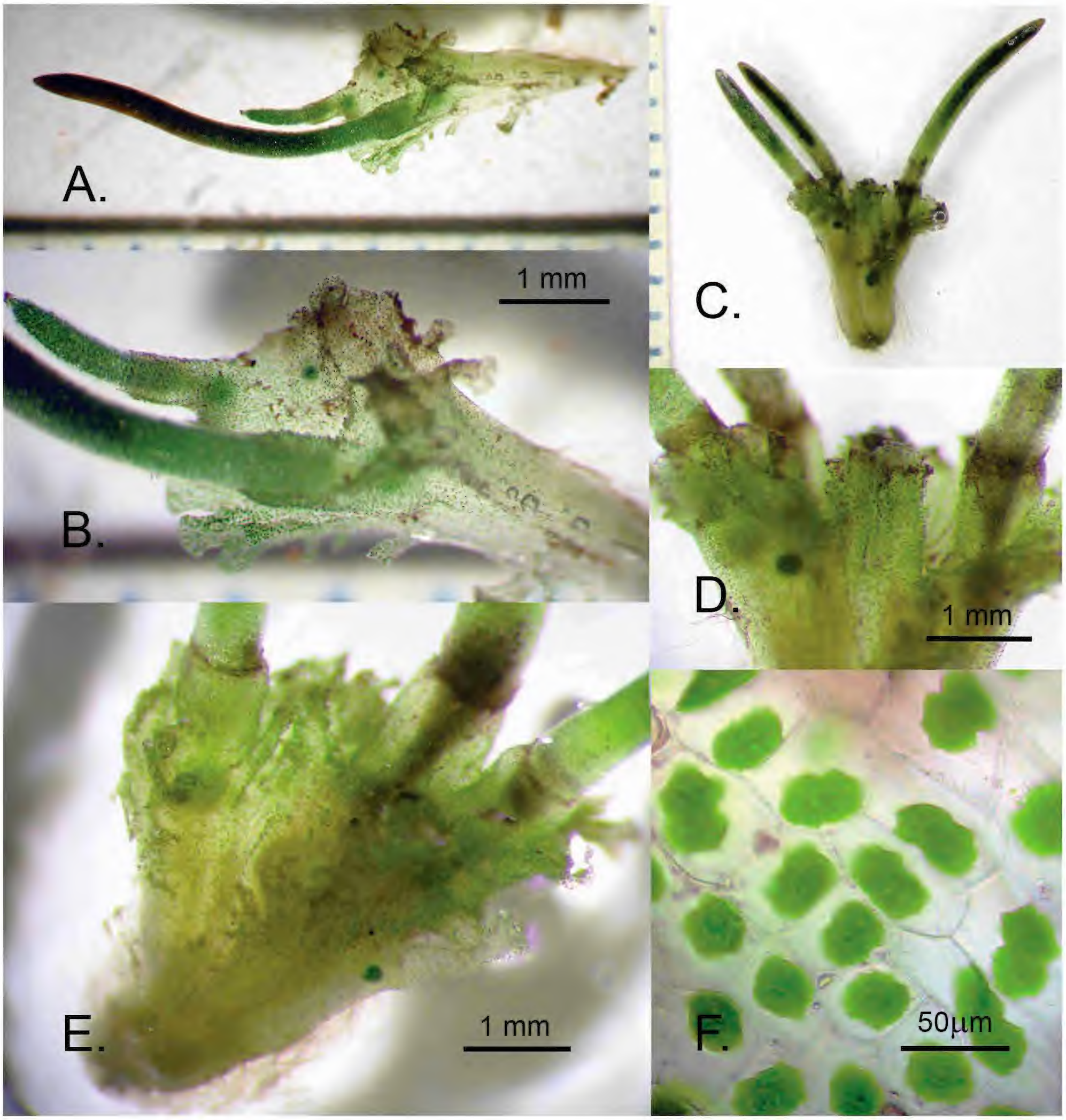

Figure 8. A–E. Whole individual plants of *Anthoceros palssoniae*. Scale divisions in A, C = 1 mm. F. Chloroplasts of the epidermal cells of the thallus of *A. palssoniae* showing a lack of a pyrenoid. (All images from *R.Palsson 398(2)* CANB). Photos by D.C. Cargill.

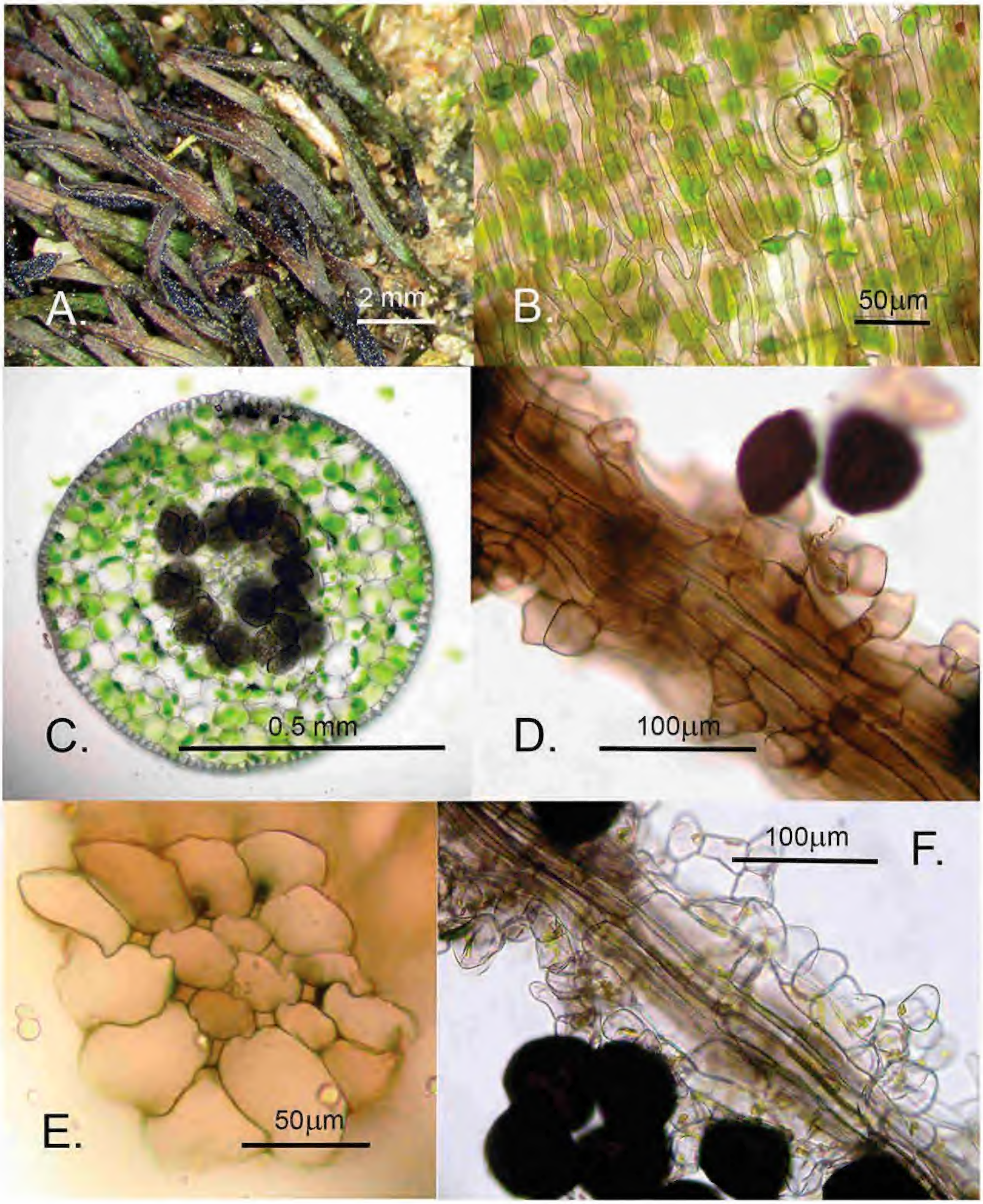

Figure 9. *Anthoceros palssoniae.* A. Fertile plants *in situ* (from *R.Palsson 398(1)* CANB). B. Epidermal cells and stomata of sporophytes. C. Cross-section through the sporophytes. D. Columella of sporophyte. E. Cross-section through columella. (Images C–E from *R.Palsson 398(2)* CANB). F. Columella with short pseudoelaters attached (from *R.Palsson 398(3)* CANB). Photos by D.C. Cargill.

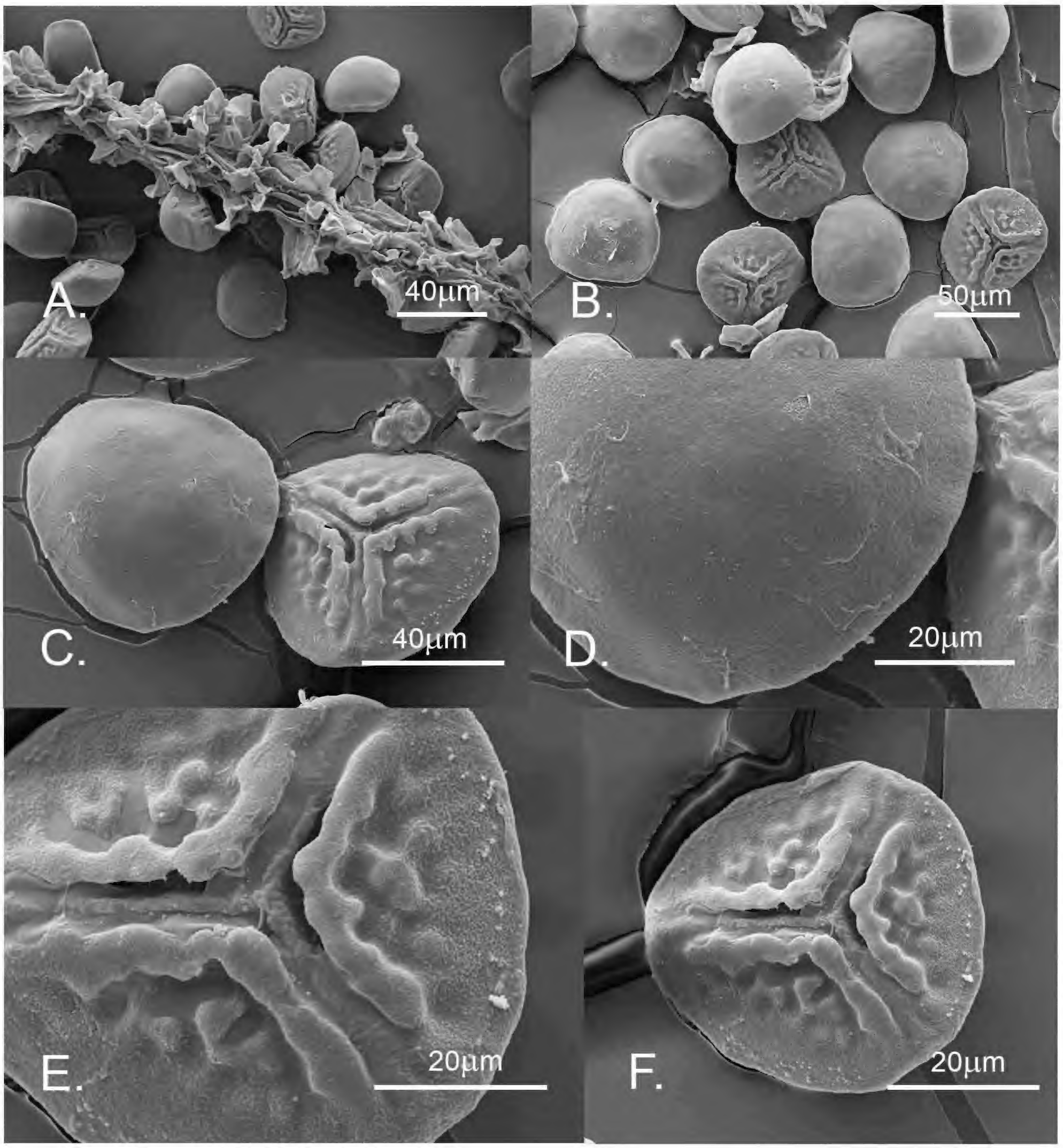

Figure 10. *Anthoceros palssoniae*. SEM images. A. Columella with spores and pseudoelaters attached. B. Group of spores showing both distal and proximal views. C. Distal and proximal view of spores. D. Close up of distal surface. E. Close-up of proximal surface. F. Proximal face of spore. (All images from *R.Palsson 398(2)* CANB). Photos by D.C. Cargill.

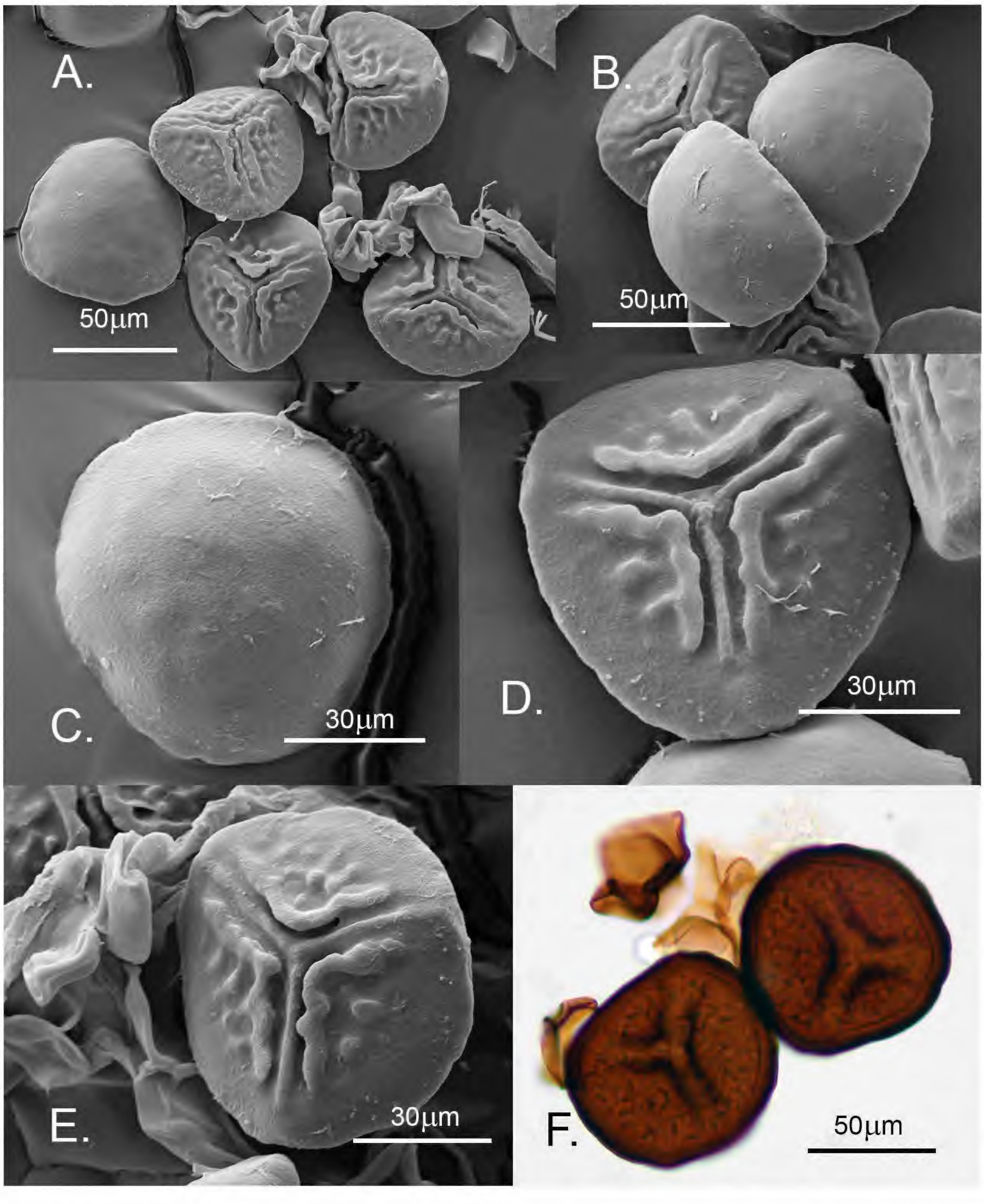

Figure 11. *Anthoceros palssoniae*. A–E. SEM images of spores and pseudoelaters. F. Light micrograph image of spores and pseudoelaters. (All images from *R.Palsson 398(2)* CANB). Photos by D.C. Cargill.

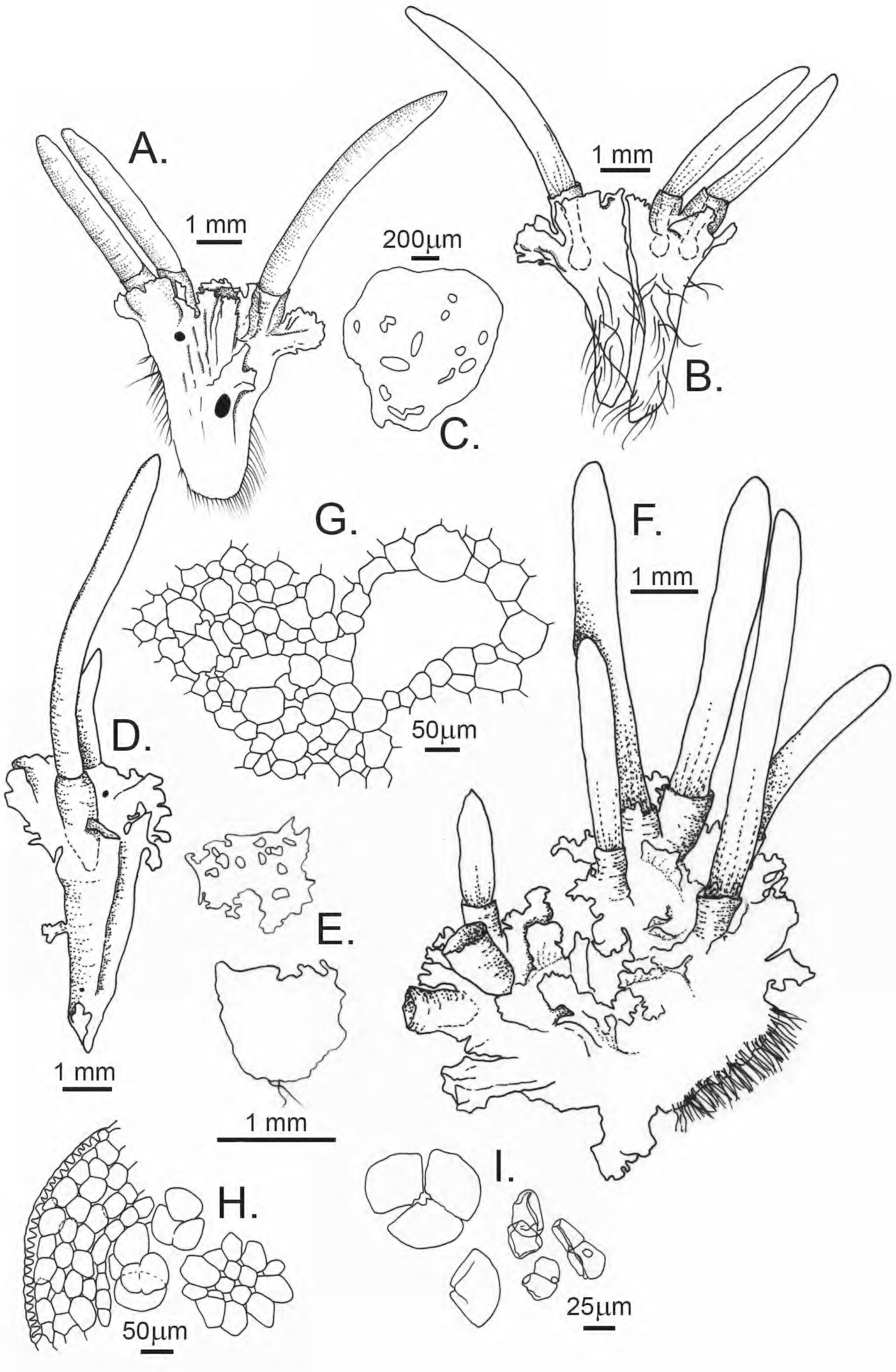

Figure 12. *Anthoceros palssoniae*. A. Dorsal view of whole fertile plant. B. Ventral view of same plant, showing that it is two plants growing vertically, side by side. C. Cross-section through the thallus of the vertically growing plants. D. Whole fertile plant. E. Cross-section through thallus. F. Whole fertile plant. G. Cross-section through thallus showing schizogenous cavities. H. Transverse section through sporophyte. I. Spores and short pseudoelaters. (A-E, G, H from *R.Palsson 398(2)* CANB). (F, I from *R.Palsson 398(1)* CANB). All drawings by D.C. Cargill.

Notes. *Anthoceros palssoniae* belongs to sect. *Fusiformes*, with spores bearing distinct smooth strips either side of the triradiate mark. Spores bear a proximal flange along the triradiate mark and wide, flat hamulate muri within each of the proximal facets like *A. apocynon*, although the muri are fewer and not as flat. The muri run into a wider, plane border around the proximal face with a micro-ornamentation of tiny papillae and baculae (Fig 9E) and an irregular sprinkling of larger papillae at the very edge (Fig 9E, F) like that of *A. apocynon*. Distally, the spores of *Anthoceros palssoniae* are smooth, readily distinguishing it from all other species in the group

when fertile. Vegetatively it stands apart from all other Australian species due to the erect growth habit, which is otherwise very similar to the Indian species *A. erectus* Kahyap. However, the thallus cells of *A. erectus* have chloroplasts with pyrenoids (S. Chantanaorrapint, *pers. comm.* 2021) and the spores have a patterned distal face.

Etymology. Named for the collector of the type, Ruth Palsson, a botanist with a particular interest in the Australian cryptogamic flora.

Distribution and habitat. Known only from the type locality in the Pilliga State Conservation Area on the North West Slopes of New South Wales. The type collection was made from *Allocasuarina luehmannii* – ironbark woodland on a fine layer of silt over pink-brown sand. Growing with other hornworts including *Anthoceros punctatus*, *A. apocynon* and *Phaeoceros* species.

Conservation status. This species has not been formally evaluated. A conservation coding of "Not Evaluated" (IUCN 2019) is therefore appropriate.

Other specimens examined. New South Wales: Pilliga State Conservation Area (SCA), Dog Proof Fence Rd, in tributary of Goona Ck, edge of creek line in plain of *Allocasuarina luehmannii* - ironbark woodland, 13 Sept. 2020, *R.L.Palsson & K.D.Durham 398(1)* (CANB 923467); *R.L.Palsson & K.D.Durham 398(3)pp.* (CANB 923469).

Anthoceros wellmanii Cargill, ***sp. nov.***

Diagnosis. Similar to *Anthoceros apocynon* with which it shares spores that are spiny on the distal face, with a smooth strip either side of the proximal triradiate mark. *Anthoceros wellmanii* differs in the type of spines, which are fewer, coarser, and larger than the numerous fine spines on the distal face of spores in *A. apocynon*.

Type: AUSTRALIA. New South Wales: North West Slopes. Yarrigan National Park, 12 km S Baradine, 33.1 km NW Coonabarabran on Baradine Rd, 21 Sept. 2010, *P.Wellman 588A.1* (holotype: CANB 923459; isotype: NSW).

?Dioicous or strongly protandrous. Plants in patches of rosettes or half rosettes, multiple dichotomous branching pattern to form half rosettes or fans, 5.0–9.0 mm long, 3.2–7.8 mm wide, lobes from 0.1–5.8 mm long, 0.1–5.1 mm wide, margins dissected into smaller lobes; plants green to brown becoming dark green to brown or black when dry. Thallus cavernous, ecostate, mid-thallus one mucilaginous cavity layer thick, gradually decreasing in thickness to the margins, plants difficult to section to describe shape in transverse section. Dorsal surface with many short lamellae and ridges. Dorsal epidermal cells polygonal, quadrate to heptagonal, 30–87.5 × 20–57.5 μm, internal cells 55–135 × 45–65 μm. Chloroplast and pyrenoid details unknown. Ventral clefts not observed. *Nostoc* colonies absent or few, scattered through ventral half of thallus, appearing as olive green dots. Rhizoids ventral, pale brown, empty or mainly granular. Specialised asexual reproduction absent. Androecium not seen. Involucre sub-erect to erect, elongate goblet-shape to cylindrical, 0.6–1.6 mm long, sometimes contracted at the base, at least one layer of mucilaginous cavities and 2–5 cell layers thick. Capsule club-shaped, emergent, 3.5–7.9 mm long, bearing two valves, frequently opening only on one side, remaining straight not twisted upon drying, becoming dark brown to black with maturity. Capsule assimilative layer 3–5 cells thick and sporogenous layer 1 tetrad layer thick, with well-developed columella ~ 16 cells (cross section of the columella not obtained) due to pseudoelaters being permanently attached. Epidermal cells of capsule elongate-rectangular, 65–184.5 × 7.5–27.5 μm, but cell walls outlining individual cells difficult to observe, walls becoming thickened with maturity, stomata present, 40–55 × 25–27.5 μm. Spores brown (RHSCC 200A brown group), globose in polar view, a compressed tetrahedral shape in equatorial view but truncated at proximal surface apex due to flanges on either side of triradiate mark, equatorial diameter 77.5–92.5 μm, polar height 45–62.5 μm. Distal face with numerous rounded, truncated or forked protuberances, frequently coalescing to form short ridges, protuberances appear as spines around the circumference of the spore and are 2.5–10 μm long; cingulum present, 2.5–10 μm wide; proximal face dominated by a flange on either side of the triradiate mark, quite wavy when mature at its margins and protrudes away from the proximal surface; the area between the flange and the triradiate mark is smooth without any ornamentation, very few small verrucae or papillae occur in each proximal facet, triradiate mark very distinct. Pseudoelaters translucent brown, difficult to measure as remaining attached to columella, very few detaching, thin-walled; 2–5 cells long, 87.5–112.5 μm in length and 20–30 μm wide, frequently branched, several branches per pseudoelater, surface smooth. Figs 2, 7, 13–14.

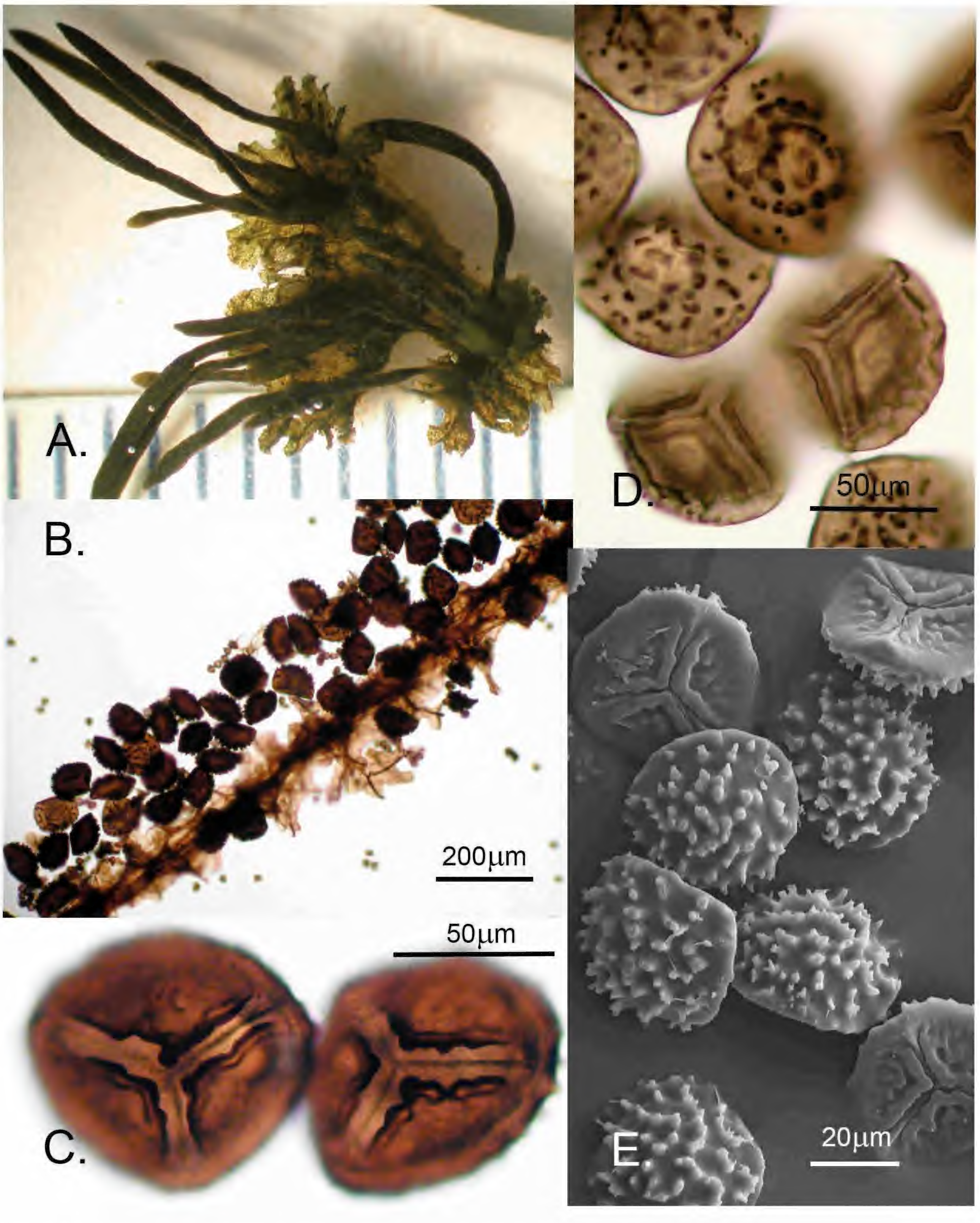

Figure 13. *Anthoceros wellmanii*. A. Whole single fertile plant. Scale divisions = 1 mm. B. Columella with pseudoelaters and spores attached. C. Proximal view of spores. D. Distal and proximal view of spores. E. SEM images of spores – distal and proximal views. (Images from *P.Wellman 588A* CANB). All photos by D.C. Cargill.

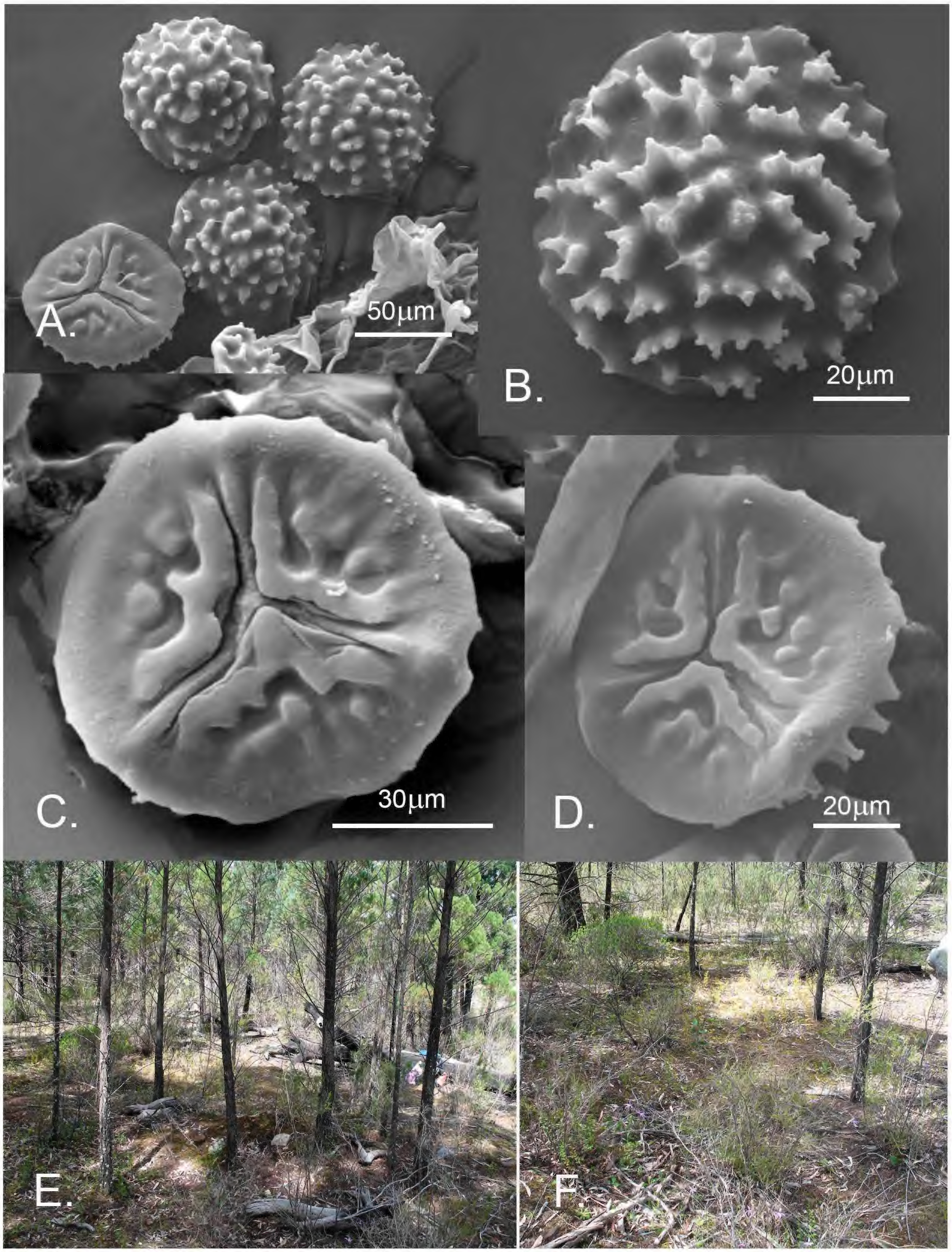

Figure 14. SEM images of spores of *Anthoceros wellmanii*. A, B. Distal views of spores. C, D. Proximal view of spores. (Images from *P.Wellman 588A.1* CANB). E, F. Habitat views of *A. wellmanii*. A–D. Photos by D.C. Cargill. E, F. Photos by P. Wellman.

Notes. The proximal face of the spores in *A. wellmannii* are very similar to those of *A. palssoniae*, with the distinct flange and few muri on the proximal facets. However, the distal face in *A. wellmannii* has spines (Figs 12D, E, 13A, B) unlike the smooth distal face of *A. palssoniae*. Spines in *A. wellmanii* are similar to those of *A. apocynon* but are fewer and larger in *A. wellmanii* as compared to *A. apocynon*. The spores of this species are also similar to two Indian species; *Anthoceros alpinus* and *A. bharadwajii* (Asthana and Srivastava 1991) and

China (Peng and Zhu 2013) and similar species from the Americas; *A. cavernosus* Steph., *A. fusiformis* Austin, *A. macounii* M.Howe and *A. orizabensis* (Steph.) Hässel (Hassel de Menendez 1990), sharing the smooth strip either side of the triradiate mark and numerous blunt spines over the distal face. However, *Anthoceros wellmanii* spores are much larger in diameter (77.5–92.5 μm) than the Indian and American species and the proximal face is distinctly different from any of the Indian or American species (Asthana and Srivastava 1991, Hassel de Menedez 1990), which are in the most part spiny.

Etymology. Named for the collector of the type material and Australian National Herbarium affiliate and Australian slime mould expert, Dr Peter Wellman.

Distribution and habitat. Known from two populations near Coonabarabran in the North West Slopes region of New South Wales. Both collections were made in disturbed habitats. The type collection (*P. Wellman 588A.1*) was made on a 4WD track and scrapings at side of track on silty soil in a *Eucalyptus* and *Callitris* woodland. The other collection (*P. Wellman 587A*) was made on a gently sloping site on silt or clay in a *Callitris* woodland under shrubs (Figs 12 E, F). Growing amongst other hornworts such as *Anthoceros punctatus*, and *Phaeoceros* sp.

Conservation status. This species has not been formally evaluated. A conservation coding of "Not Evaluated" (IUCN 2019) is therefore appropriate.

Other specimens examined. New South Wales. 17 km NW Coonabarabran on Baradine Rd, possibly in Yearinan State Forest, between road and railway line, 21 Sept. 2010, *P. Wellman 587A*.3 (CANB 923460).

Acknowledgments

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References

Asthana AK, Srivastava SC (1991) Indian hornworts (a taxonomic study). *Bryophytorum Bibliotheca* 42: 1–158.

Dawes TN, Villarreal A JC, Szövényi P, Bisang I, Li F-W, Hauser DA, Quandt D, Cargill DC, Forrest LL (2020). Extremely low genetic diversity in the European clade of the model bryophyte *Anthoceros agrestis*. *Plant Systematics and Evolution* 306: 49. https://doi.org/10.1007/s00606-020-01676-6

Grolle R (1976) Verzeichnis der Lebermoose Europas und benachbarter Gebiete. *Feddes Repertorium* 87: 171–279. https://doi.org/10.1002/fedr.19760870303

Hässel de Menéndez GG (1990) Las especies de *Anthoceros* y *Folioceros* (Anthocerotophyta) de America del Norte, Sud y Central; la ornamentacion de sus esporas y taxonomia. *Candollea* 45: 201–220. https://www.e-periodica.ch/digbib/view?pid=can-002%3A1990%3A45%3A%3A434#206

IUCN Standards and Petitions Committee (2019) *Guidelines for Using the IUCN Red List Categories and Criteria*. Version 14. http://www.iucnredlist.org/documents/RedListGuidelines.pdf (Accessed March 2021)

McCarthy P (2006) Catalogue of Australian Liverworts and Hornworts. *Flora of Australia Supplementary Series 21*. Australian Biological Resources Study: Canberra, Australia

Peng T, Zhu R-L (2013) A revision of the genus *Anthoceros* (Anthocerotaceae, Anthocerotophyta) in China. *Phytotaxa* 100: 21–35. http://dx.doi.org/10.11646/phytotaxa.100.1.3

Proskauer J (1958) Nachtrag zur Familie Anthocerotaceae. In K. Muller, *Die Lebermoose Europas*: *Rabenhorst's Kryptogamen-Flora* (3rd edn) pp. 1303–1319. Akademische Verlagsgesellsch: Leipzig

Sérgio C (1987) Contribuicâo para o estudo taxonómico e fitogeográfico de *Anthoceros caucasicus* Steph. na Península Ibérica e Macaronésia. *Actas del VI Simposio National de Botánica Criptogámica* pp. 605–614. Granada

Vaughn, KC, Ligrone, R, Owen, HA, Hasegawa, J, Campbell, EO, Renzaglia, KS Monge-Najera, J (1992) The anthocerotes chloroplast: a review. *New Phytologist* 120: 169–190. https://doi.org/10.1111/j.1469-8137.1992.tb05653.x

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Tristaniopsis flexuosa (Myrtaceae), a new species from ultramafic soils in the Philippines

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Abstract

A new species of *Tristaniopsis* (Myrtaceae) from the Philippines, *Tristaniopsis flexuosa* Fernando & Peter G.Wilson, is formally described and illustrated. At present, the species is known only from a single locality in upper montane forest in extreme ultramafic habitat and we provide an assessment of its conservation status. Its relationship to other Malesian species of *Tristaniopsis* is discussed, and a key to the identification of the Philippine species provided.

Introduction

Tristaniopsis Brongn. & Gris is a genus of c. 50 species, with a distribution extending from Myanmar and Thailand in the north, through Malesia and extending to eastern Australia and New Caledonia. According to the *Philippine Plants* website (Pelser et al. 2011 onwards) only four named species of *Tristaniopsis* are recorded from the Philippines, all first described before 1920. They were all named by Elmer D. Merrill as species of the genus *Tristania* R.Br. and were subsequently transferred to *Tristaniopsis* by Wilson and Waterhouse (1982). Given the diversity of habitats in the Philippines, it is likely that further species are yet to be discovered. In Borneo, which has a much larger land area, it is estimated that there are well over 20 species, many of which are undescribed (Berhaman 2011).

During preliminary floristic field surveys (Fernando et al. 2017) and a later, more detailed, study of the forest habitat types on Dinagat Island (Lillo et al. 2019), a distinctive vegetation type was recorded in upper montane forest on ultramafic substrates. This forest formation consists of shrubs and small trees attaining no more than 3 meters in height. In this distinctive habitat, several unnamed taxa were identified, including a rather distinctive species of *Tristaniopsis*. Two of the other four *Tristaniopsis* species recorded from the Philippines are also known to occur on ultramafic substrates but this one is much smaller, has an unusual growth habit, and occurs at a much higher elevation. We therefore recognise this as a new species, *Tristaniopsis flexuosa*.

Plants were studied in the field and specimens collected by the first author. Initial observations were made on fresh material and confirmed and supplemented by additional measurements of dried herbarium material.

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Key to the Philippine species of *Tristaniopsis*

1 Leaves to 1.5 cm long; peduncles 4–6 mm long ..... ***T. flexuosa***

1* Leaves >3.5 cm long; peduncles >10 mm long..... 2

2 New growth and inflorescences densely yellowish-brown tomentose ..... ***T. oblongifolia***

2* New growth and/or inflorescences puberulent or finely pubescent..... 3

3 Lamina narrowing to a rounded-auriculate base; petiole 2–3 mm long ..... ***T. littoralis***

3* Lamina decurrent; petiole c. 10 mm long..... 4

4 Inflorescences 5–10 cm long, upper branches lax; flowers c. 2 mm across ..... ***T. micrantha***

4* Inflorescences 4–6 cm long, upper branches compact; flowers c. 4 mm across ..... ***T. decorticata***

Description

Tristaniopsis flexuosa Fernando & Peter G.Wilson, **sp. nov**.

Type: Philippines: Dinagat Island, Municipality of Loreto, Mount Redondo, 876 m elevation, dwarf forest on ultramafic soil, *E.S. Fernando 4186*, 1 Sep 2016 (holotype PNH; isotypes LBC, NSW).

Diagnosis: Differs from all other named Philippine taxa of *Tristaniopsis* in having distinctive flexuose stems, relatively small leaves with obtuse to rounded apex, and a compact inflorescence.

Shrub or small *tree* to *c.* 2.5–3 m tall, stem *c.* 5–6 cm diameter, much branched and with flexuose stems. *Bark* smooth, grey, flaking off to reveal red-brown under-bark. *Twigs* not conspicuously angular; young stems and leaves with a loose indumentum of pale, spreading hairs, glabrescent. *Leaves* broadly elliptic to obovate, 12–18(–24) mm long, 5–10(–14) mm wide, the smaller leaves tending to be at the base of each leaf cluster on the twig; juvenile leaves densely pubescent on both surfaces and along the midrib and margins, mature leaves generally glabrescent; petiole 1–2 mm long, sometimes indistinct, or appearing winged; base cuneate to attenuate; apex obtuse to rounded; secondary veins 7–10 on each side of the midrib, not distinct in fresh material; midrib slightly sunken on the adaxial surface, raised on the abaxial surface; margins slightly thickened and revolute, intramarginal vein distinct. *Inflorescence* a compact dichasium, subterminal or terminal, usually shorter than the leaves; peduncle 4–6 mm long, densely pubescent. *Flowers* creamy white to pale yellow, up to 7–11 mm across; pedicel 2–3 mm long, pubescent; hypanthium 3–8 mm across, 2–3 mm deep, the lobes 0.5–1 mm long x 1–2 mm wide; petals 5, each 2.5–4 mm across; stamens yellowish, 3 opposite each petal, joined at the base, glabrous; middle stamen with filament to 1 mm long, those of side stamens to 0.5 mm long; anthers basifixed, 0.3 mm long; stigma capitate; style 0.5–1.5 mm long; ovary half-inferior, 3 mm diameter; immature fruit subglobse, reddish, with prominent stylar scar, the surface smooth and glossy; mature capsule and seeds not known. **Fig. 1**

Distribution: Endemic to the Philippines. Thus far known only from the type locality on Mount Redondo, Dinagat Island.

Etymology: The specific epithet refers to the distinctive flexuose stems (Fig. 1A, B).

Habitat: Occurs in dense dwarf forest, 1–2 m tall, on ultramafic soils, on gentle slopes, 840–879 m elevation. Rather uncommon at site.

Other specimens examined: PHILIPPINES: Dinagat Island, Municipality of Loreto, Mount Redondo, 846 m elevation, *E.S. Fernando 3836B*, 29 Sep 2015 (LBC, PNH); 849 m elevation, *E.S. Fernando 4176*, 1 Sep 2016 (LBC, NSW, PNH, SING).

Affinities: *Tristaniopsis flexuosa* does not show clear affinities to any other Philippine species. Morphologically, it most nearly approaches *Tristaniopsis elliptica* (Stapf) Peter G.Wilson & J.T. Waterh., a species from Borneo that occurs on ultramafic substrates at some locations, particularly in the vicinity of Mount Kinabalu. *Tristaniopsis elliptica* also has relatively small, obtuse leaves and three stamens per fascicle. It is also reported to have a 'crooked' habit in some cases (Ashton & Teo 2011). However, *T. elliptica* is a much larger tree with a broader bole, to *c.* 20 m tall and 30–40 cm diameter. It has larger leaves that are commonly 5 x 2.5 cm (range 3–10 x 1.5–3.5) while in *T. flexuosa* they are mostly in the range of 1.2–1.8 x 0.5–1 cm, and the secondary lateral veins are more numerous (20–24 compared with 7–10 in *T. flexuosa*). The two species are likely to be sister taxa but their respective geographic areas are about 1000 km apart and have been separated since the formation of the Sulu Sea from the early to mid-Miocene through to the late Miocene when it reached its present extent, c. 9 Ma (Lai et al. 2021).

Fig. 1. *Tristaniopsis flexuosa* Fernando & Peter G.Wilson. **A, B.** Habit and close-up of branching and stems showing parts of the outer bark peeling off, revealing reddish-brown under-bark; **C.** Leafy part of crown showing inflorescences; **D.** Close-up of inflorescences and flowers, showing the three stamens per fascicle and the fine, spreading indumentum; **E.** Immature fruit. A–C from *E.S. Fernando 4186*; D from *E.S. Fernando 4176*; E from *E.S. Fernando 3836B*. Photos: Edwino S. Fernando.

Notes: Shrubby plants of *Tristaniopsis flexuosa* in its type locality were about 1 m tall, but already flowering and fruiting. The larger plants grow to about 2.5–3 m tall, often protruding through the canopy of the dwarf forest and readily distinguishable owing to their open crowns (Fig. 1A). Some of the shrubs and small trees associated with this new species in the dense dwarf forest include *Dacrydium beccari* Parl. (Podocarpaceae), *Fagraea gitingensis* Elmer (Gentianaceae), *Leptospermum amboinense* Blume (Myrtaceae), *Medinilla theresae* Fernando (Melastomataceae), *Psychotria surigaoensis* Sohmer & A.P.Davis (Rubiaceae), *Rhodomyrtus surigaoensis* Elmer (Myrtaceae), *Scaevola micrantha* C.Presl (Goodeniaceae), *Tarenna elongata* Merr. (Rubiaceae), *Ternstroemia gitingensis* Elmer (Pentaphylacaceae), and two pitcher plants, *Nepenthes mindanaoensis* Sh.Kurata and *Nepenthes erucoides* A.S.Rob. & S.G.Zamudio (Nepenthaceae), among many others.

Ultramafic substrates are known from other mountain ranges in the southern Philippines, but the habitats differ, and *Tristaniopsis flexuosa* has not been recorded from any of them. Mount Hamiguitan on the Pujada Peninsula in south-eastern Mindanao is ultramafic and has dwarf mossy forest but this is found at 1160–1600 m elevation, nearly twice as high as Mount Redondo. It is a UNESCO World Heritage site and relatively well-collected. Mount Hilong-hilong in north-eastern Mindanao is probably ultramafic but does not have a dwarf forest at the summit (c. 2100 m), only a typical mossy forest.

Provisional conservation assessment: The entire area of dwarf forest on Mount Redondo above 750 m elevation is estimated at only 5.27 km^2 (Lillo et al. 2019) and *Tristaniopsis flexuosa* is known thus far only from this single location. Its Extent of Occurrence (EOO) is, thus, less than 100 km^2 and its Area of Occupancy (AOO) less than 10 km^2, all within the threshold of IUCN's Critically endangered (CR) category. The Mount Redondo area is still within a mineral reservation (for chromite and associated mineral deposits, including nickel) and parts of it have previously been subjected to open pit mining for chromite. The species will be at serious risk should mining be allowed to continue on this site. A continuing decline is inferred or projected in the (i) extent of occurrence; (ii) area of occupancy; and (iii) area, extent and/or quality of habitat due to the possibility of further mining. Following IUCN (2012) and the *Guidelines for Using the IUCN Red List Categories and Criteria* (IUCN Standards and Petitions Subcommittee 2019), we regard this species as Critically Endangered CR B1ab(ii,iii)+2ab(i,ii,iii).

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References

Ashton PS, Teo S (2011) *Tristaniopsis*. In: Soepadmo E, Saw LG, Chung RCK, Kiew R (eds) *Tree Flora of Sabah and Sarawak* 7: 308–322. Forest Research Institute Malaysia, Kepong.

Berhaman A (2011) Taxonomic Revision and Phylogeny Study of the Genus *Tristaniopsis* (Myrtaceae) of Borneo. Unpublished dissertation, University of Aberdeen, U.K.

Fernando ES, Arbolonio RB, Lillo EP (2017) *Forest Flora of Dinagat Island: An Introductory Guide*. 128p. Department of Environment and Natural Resources (DENR), Philippines.

IUCN (2012) *IUCN Red List Categories and Criteria*. Version 3.1, 2nd edition. Gland, Switzerland and Cambridge, U.K. www.iucnredlist.org/technical-documents/categoriesand-criteria (accessed 6 September 2021)

IUCN Standards and Petitions Subcommittee (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Subcommittee http://www.iucnredlist.org/documents/RedListGuidelines.pdf (accessed 6 September 2021)

Lai C-K, Xia X-P, Hall R, Meffre S, Tsikouras B, Rosana Balangue-Tarriela MI, Idrus A, Ifandi E, Norazme NA (2021) Cenozoic evolution of the Sulu Sea Arc-Basin system: An overview. *Tectonics* 40(2): e2020TC006630.

Lillo EP, Fernando ES, Lillo MJ (2019) Plant diversity and structure of forest habitat types on Dinagat Island, Philippines. *Journal of Asia-Pacific Biodiversity* 12: 83–105.

Pelser PB, Barcelona JF, Nickrent DL (eds.). (2011 onwards) *Co's Digital Flora of the Philippines*. https://www.philippineplants.org/Families/Myrtaceae.html (accessed 2 September 2021)

Wilson PG, Waterhouse JT (1982) A review of the genus *Tristania* R.Br. (Myrtaceae): a heterogeneous assemblage of five genera. *Australian Journal of Botany* 30: 413–446.

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A new species of *Rhodomyrtus* (Myrtaceae) with brochidodromous venation from north-eastern Queensland, Australia

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Abstract

Rhodomyrtus verecunda A.J.Ford & Peter G.Wilson from north-eastern Queensland, Australia, is formally described and illustrated. Notes on habitat, distribution and conservation status are provided, as are details of how it is distinguishable from *R. macrocarpa*, the only other non-acrodromous species of the genus in the region. A revised key to the species of *Rhodomyrtus* in Australia is also presented.

Introduction

The genus *Rhodomyrtus* (DC.) Rchb. (Myrtaceae) is distributed from India and eastwards through southern Asia to New Caledonia and the Solomon Islands, including eastern Australia (Snow *et al.* 2008). When Scott (1978) revised the genus there were 11 species with several infraspecific taxa recognised. The total number of species has grown steadily since then and it currently stands at 23 species (Snow and Cantley 2010). The island of New Guinea is seen as the centre of diversity (13 spp.), followed by Australia with seven species (Snow *et al.* 2011).

Rhodomyrtus has traditionally been assigned to a broadly defined subtribe Myrtinae within the tribe Myrteae, based on the occurrence of seeds with a hard, bony testa and C-shaped or spiral embryos (e.g. Landrum and Kawasaki 1997). More recently, however, Lucas *et al.* (2019) proposed a new subtribal classification for the Myrteae, with *Rhodomyrtus* and many other Australasian genera (e.g. *Archirhodomyrtus* (Nied.) Burret, *Decaspermum* J.R. & G.Forst., *Gossia* N.Snow & Guymer, *Pilidiostigma* Burret and *Rhodamnia* Jack) placed in a new subtribe Decasperminae E.Lucas & T.Vasc.

The likelihood that *Rhodomyrtus* is not a single lineage has been considered in the literature by several authors (e.g. Wilson *et al.* 2005, Wilson 2011 and Snow *et al.* 2011), with the consensus being that it is probably polyphyletic. However, despite morphological data strongly suggesting polyphyly, current molecular analyses, based on ITS data only, are inconclusive (Snow *et al.* 2011). These molecular analyses show species of *Rhodomyrtus* clustered in two clades intermixed with species of *Octamyrtus* Diels, *Kanakomyrtus* N.Snow and *Archirhodomyrtus*.

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Morphological characters thought to be diagnostic of *Rhodomyrtus* by many authors (e.g. Scott 1978, Guymer 1991) have included: 5-merous flowers, axile placentation, baccate fruit and seeds with a sclerotic outer testa separated by a false septa. However, the enigmatic *Rhodomyrtus macrocarpa* Benth. has an ovary reduced to a single loculus with parietal placentation. In the morphology-based phenogram of Snow *et al.* (2011, Fig. 1, p. 393), *R. macrocarpa* is surprisingly sister to *Kanakomyrtus dawsoniana* N.Snow despite the significant floral morphological differences between the two.

Photographs of mature fruit from an unusual species of Myrtaceae from the Cape Tribulation area of north-east Queensland were sent to the first author by Tim Hawkes for identification. Discussions between the two led to a successful outing where specimens with flowers and mature fruit were collected and assessed. Although resembling *R. macrocarpa* in gross morphology, examination of herbarium specimens found significant differences, including the first occurrence of brochidodromous leaf venation within *Rhodomyrtus* in Australia. Both flowering and fruiting material has enabled the confirmation that Hawkes' puzzle represented an undescribed species, which we describe below as *R. verecunda* A.J.Ford & Peter G.Wilson.

Material and Methods

This study of *Rhodomyrtus* was exclusively based on the examination of herbarium specimens held at NSW and CNS including spirit (alcohol) collections at CNS. In addition, fieldwork by the first author enabled the collection of fresh material for morphological assessment and DNA analysis, and pertinent ecological observations and data for conservation assessment.

Taxonomy

Rhodomyrtus verecunda* A.J.Ford & Peter G.Wilson, *sp. nov.

Type: Queensland: Cook District: Daintree National Park, Noah Island on bank of Noah Creek, 13 June 2016, *A. Ford 6569, T. Hawkes* and *B. Gray* (holotype: BRI; isotypes: CNS, MEL, NSW, SING).

Diagnosis: Differs from *Rhodomyrtus macrocarpa* in its leaf venation (brochidodromous versus eucamptodromous), inflorescence type (solitary versus triads or botryoids), hypanthium shape and texture (funnel-shaped and smooth versus cylindrical and ribbed), style length (7.5–8 mm versus 4.5–5 mm), placentation type (axile versus parietal), ovary structure (bilocular versus unilocular) with fewer ovules per flower (4–6 versus numerous).

Large shrubs to small trees 3–5 m tall. Bark flaky (layered), outer blaze fawn, fibrous; a dark brown layer apparent between the dead bark and the living bark layer. *Branchlets* green when freshly expanded, turning brownish and finally creamy to creamy-brown, epidermis glandular especially on youngest growth, moderately sericeous (hairs whitish and antrorse), strongly compressed on youngest growth and becoming terete with age, each side bearing 2 longitudinal grooves separated by a raised midline, swollen at nodes, terminal bud densely sericeous. *Leaves* opposite, decussate, evenly distributed along branchlets, discolorous when fresh but scarcely so when dry, venation brochidodromous (occasionally eucamptodromous proximally), both surfaces matte. Colleters (type "A" stipule sensu Snow *et al.* 2003) deciduous to moderately persistent, *c.* 0.25 mm long, filiform, dark maroon, usually 8 per leaf. Petioles purple, 2.0–4.1 mm long, *c.* 1.5 mm wide (appearing much longer due to the extremely attenuate leaf bases), flat or nearly so adaxially, strongly rounded abaxially, sericeous, longitudinally striated when dry. Leaf blades elliptic-obovate to obovate-spathulate, (38–)48–108 mm long, (12–)18–35 mm wide, length to width ratio 2.1–3.2(–4): 1, coriaceous; base exceedingly attenuate and narrowing very gradually towards the proximal part of petiole, margin flat when fresh but slightly recurved near petiole when dried; apex variable, from shortly acuminate to acute, obtuse or retuse; acumen glabrescent, usually densely clothed in antrorse silky white hairs, containing a single oil gland so that, without magnification, it can resemble a mucro; adaxial surface moderately but persistently sericeous, more densely so on the midvein; midvein slightly raised in a shallow depression when fresh but appearing flush when dry, secondary and tertiary veins ± flush when fresh but strongly raised when dry; abaxial surface sparsely and persistently sericeous, more so proximally and on the midvein; oil glands common, visible with magnification, erupting the surface on both abaxial and adaxial surfaces; midvein strongly raised when fresh or dry, secondary and tertiary veins raised when fresh or dry; 7–11 secondary veins on each side of the midvein, intramarginal vein absent. *Inflorescence* a solitary flower (monad), one per axil; anthopodia present, metaxyphylls absent; peduncles 5.5–7 mm long, *c.* 0.6 mm diameter proximally, angular distally, longitudinally striated when dry, sericeous, moderately clothed in short

white antrorse hairs, oil glands common. Bracteoles 2, 2.1–3.4 mm long, 0.4–0.5 mm wide, oblong, erect in bud, sericeous, moderately clothed in short white antrorse hairs, longitudinally striated, adaxially sulcate, deciduous to moderately persistent, occasionally persisting on immature fruit, oil glands common. *Hypanthium* 6.5–8 mm long, funnel-shaped, moderately and shortly sericeous, smooth (not ribbed), not extending beyond ovary. *Calyx* lobes 5, unequal, green, broadly obtuse, 2.5–3 mm long, 5–6 mm wide, ± reniform, moderately sericeous on both surfaces, becoming tomentose-sericeous towards the margins, ciliate, spreading at anthesis. *Petals* 5, white, 10.5–12 mm long, 10.5–11.5 mm wide, cupular, obovate, prominently glandular, glabrous or nearly so on both surfaces, sparsely sericeous abaxially near apex, ciliate. *Stamens* numerous, 5–7-seriate; filaments filiform 5.6–10.1 mm long, leaving conspicuous scars around the ovary; anthers *c*. 0.4 mm long, ellipsoid, dehiscing through longitudinal slits, basifixed, connective tipped with an apical gland. *Ovary* apex hairy. Style sericeous throughout, 7.5–8 mm long, stigma peltate. Ovary 2-locular; placentation axile; ovules 2–3 per locule, ascending. *Fruit* indehiscent, baccate, the flesh leathery (not 'juicy'), globose-pyriform, 20–21 mm long, 16–16.5 mm diameter, green proximally (lower 25%) and purple-red distally (upper 75%), surface smooth (not ribbed) and puberulent, glandular, calyx lobes erect, peduncle not enlarged or elongating markedly. Seeds 2 per fruit, testa brown with radial markings, bony-fibrous, hemispheroidal, 7.5–8 mm long, 4.5–7 mm wide, the placental face flat; embryo glandular, circinate, radicle longer and thicker than cotyledons. Specific wood density 714 kg/m^3. Fig. 1.

Fig. 1. *Rhodomyrtus verecunda*. A. Habit of flowering branchlet; B. Mature fruit and leaves with purple petioles; C. Riparian habitat along Noah Creek; D. Wind-sheared ridge habitat on Mt Sorrow (Photo Credits; CSIRO, Andrew Ford).

Distribution: *Rhodomyrtus verecunda* is endemic to the Wet Tropics bioregion (Department of Environment 2012) in north-eastern Queensland, Australia, where it is currently only known from a restricted area in the very high rainfall zone (>3000 mm per annum) between the Daintree River, Cape Tribulation and Mt Pieter Botte (north of Cairns) (Fig. 2).

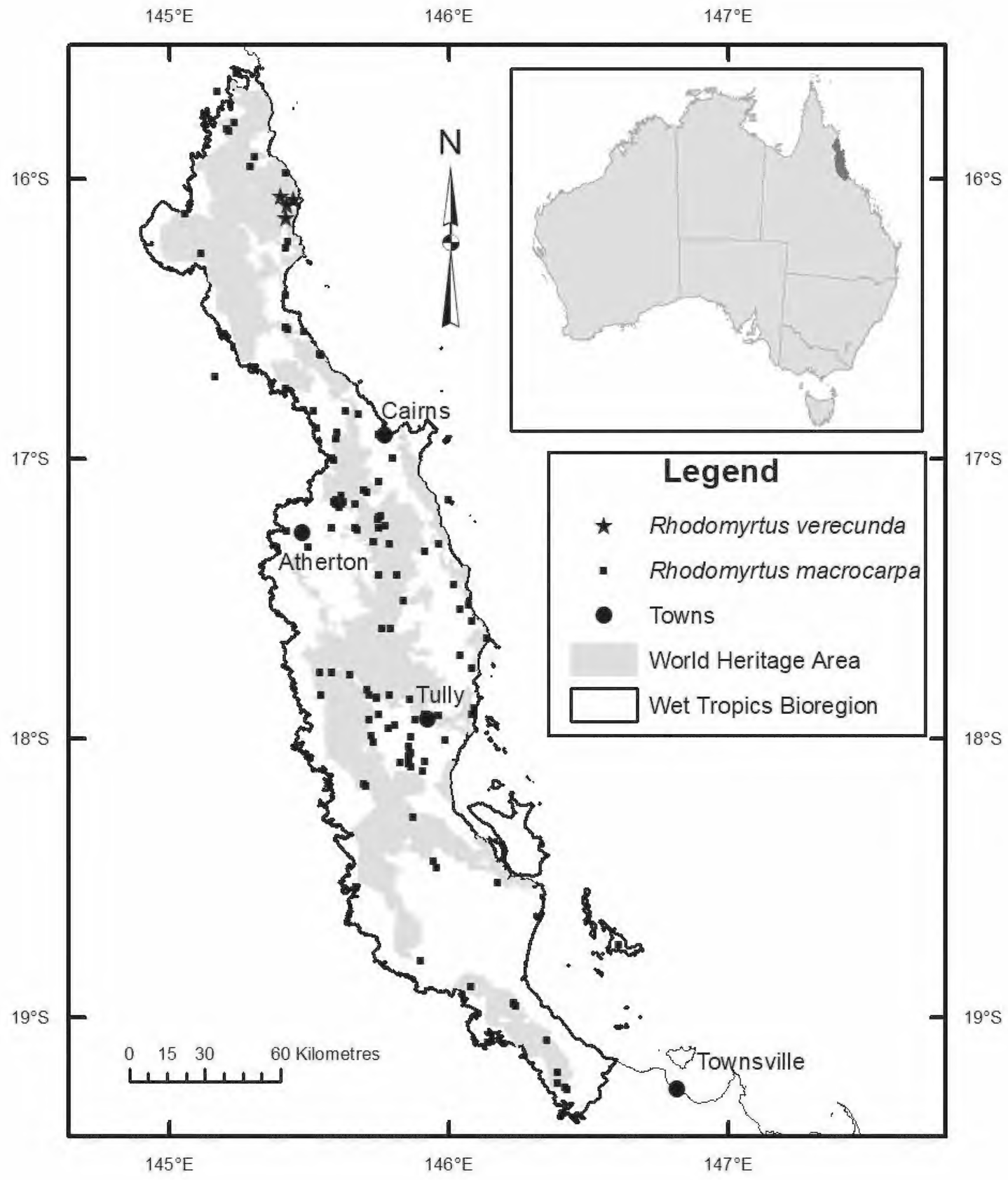

Fig. 2. Distribution of *Rhodomyrtus verecunda* and *Rhodomyrtus macrocarpa* in north-east Queensland, Australia (*R. macrocarpa* occurs from Central Queensland to Cape York and extends into New Guinea, but for comparative purposes only occurrences in north-east Queensland are shown.)

Habitat and Ecology: This species is known from three distinctive rainforest vegetation types:

1. Notophyll rainforest along creekbanks associated with large granite boulders (Fig. 1c). Canopy dominated by *Xanthostemon chrysanthus*. Smaller trees include: *Gymnostoma australianum, Neorites kevediana, Dissiliaria tuckeri, Choriceras majus* and *Atractocarpus sessilis.* Shrubs: *Dinghoua globularis, Phyllanthus hypospodius, Hypsophila dielsiana, Schistocarpaea johnsonii* and *Medicosma sessiliflora*. The ground layer is dominated by *Lomandra hystrix.*

2. Microphyll rainforest on ridges of metasediments (Fig. 1d). Canopy heavily wind-sheared and dominated by: *Ceratopetalum iugumensis, Balanops australiana*, *Elaeocarpus ferruginiflorus*, *Psydrax montigena*, *Musgravea stenostachya*, *Halfordia scleroxyla* and *Trochocarpa bellendenkerensis*. Shrubs and small trees: *Argophyllum cryptophlebum*, *Garcinia brassii*, *Alyxia orophila*, *Pittosporum rubiginosum*, *Wendlandia inclusa*, *Linospadix* sp., *Chionanthus axillaris, Tasmannia membranea*, *Psychotria* spp., *Crispiloba disperma* and *Lenbrassia australiana* var. *glabrescens*. The ground layer is dominated by *Romnalda ophiopogonoides.*

3. Notophyll rainforest associated with granite outcrops, often near creekbanks. Canopy trees include: *Agathis atropurpurea, Sphalmium racemosum, Syzygium hemilamprum* subsp. *orophilum, Niemeyera discolor, Gymnostoma australianum, Sarcopteryx reticulata* and *Sloanea australis.* Shrubs and small trees include: *Phyllanthus hypospodius*, *Medicosma heterophylla, Xanthostemon graniticus, Rhodamnia sessiliflora, Chionanthus axillaris, Atractocarpus hirtus* and *Polyscias bellendenkerensis.*

The recorded altitudinal range is 20–720 m, with most collections above 600m (rainforest types 2 and 3 above).

Phenology: Flowering is recorded for June only, although buds recorded in December and mature fruit is only known from June. Immature fruit has been observed in May, August and September. Given the wide range of observations of fertile material, it is possible that flowering and fruiting occurs sporadically throughout the year and varies significantly between individuals within a population.

Conservation Status: *Rhodomyrtus verecunda* is currently only known from Daintree National Park, between the Daintree River and Cape Tribulation, north of Cairns. Its conservation status has not been assessed formally according to IUCN (2019) guidelines. It is known from five collections representing four locations and its extent of occurrence (EOO) is only 18 km^2. At present, there is no evidence of decline in population size, but further fieldwork is needed desperately to assess recruitment and population numbers from each of the known locations. We recommend a status of *Not Evaluated* (IUCN 2019) until the above information is acquired and related to any possible future threats, including any changes to the highly localised and unique climate that this species inhabits.

Etymology: The epithet *verecunda*, from the Latin *verecundus* (shy, modest, bashful), is a reference to this species being so similar to *R. macrocarpa*, being essentially hidden in plain sight, and having relatively few ovules and seeds compared to most other species of *Rhodomyrtus*.

Affinities: Amongst Australian species, *Rhodomyrtus verecunda* is morphologically closest to *R. macrocarpa* and, in fact, the paucity of anthetic flowering material or collections of mature fruit has resulted in it being included within the concept of *R. macrocarpa* since the 1980s. Both species have bark that is cream-coloured and flaky, and leaves that are elliptic to obovate-spathulate with purple petioles. However, even sterile herbarium material can be readily identified using leaf venation alone. A comparison of diagnostic differences between *R. verecunda* and *R. macrocarpa* is provided in Table 1.

Table 1. Morphological comparison between *Rhodomyrtus verecunda* and *Rhodomyrtus macrocarpa*.

	R. verecunda	*R. macrocarpa*
Leaf venation	brochidodromous	eucamptodromous
Inflorescence type	solitary	triads or botryoids
Hypanthium shape	funnel-shaped	cylindrical
Hypanthium texture	smooth	ribbed
Style length (mm)	7.5–8	4.5–5
Placentation type	axile	parietal
Ovule number per flower	4–6	numerous (*c.* 20)
Fruit shape	globose-pyriform	ellipsoidal-torulose
Fruit base	cuneate	obtuse

In the wider Australasian region, *R. verecunda* shows some similarity to the pinnatinerved *R. elegans* (Blume) A.J.Scott from New Guinea and the Moluccas, but that species also has eucamptodromous venation. According to the key provided by Snow and Cantley (2010), two recently described species from Papua New Guinea, *R. kaweaensis* N.Snow and *R. mengenensis* N.Snow, appear to show a much closer relationship to *R. verecunda* based on the shared occurrence of terete fruits and brochidodromous venation.

Notes: Embryos of *Rhodomyrtus verecunda* and *R. macrocarpa* are both minutely glandular and strongly circinate, and resemble the embryo illustrated in Landrum and Kawasaki (1997, Fig. 6H). The same embryo type also occurs in *R. guymeriana* N.Snow & J.P.Atwood and *R. elegans* (Snow *et al.* 2008). A membranous layer, resembling a tissue-paper thickness skin, also surrounds the embryo of all four species. A conspicuous vascular core, as illustrated by Landrum and Stevenson (1986, Fig. 1), is clearly seen in an embryo cross section at the swollen end from seeds of *Rhodomyrtus verecunda* and *R. macrocarpa*.

The presence of endosperm in *Rhodomyrtus* previously has only been reported for the New Guinean endemic *Rhodomyrtus guymeriana* (Snow *et al.* 2008), where they record endosperm as "gelatinous but scant". In both *R. macrocarpa* and *R. verecunda* this gelatinous material can be found adjacent to the cotyledonary end of the embryo in fruits that are immature. It is not known whether this endosperm persists in any mature seeds, so we support the position of Snow *et al.* (2008) calling for more detailed studies on the embryology and seed status within *Rhodomyrtus*.

Although the fruit length of *R. verecunda* and *R. macrocarpa* do not overlap (20–21 mm versus 25–60 mm), occasional fruit of *R. macrocarpa* can be shortly ellipsoidal and approach the overall dimensions of *R. verecunda*:

an illustration of *R. macrocarpa* in Cooper (2004; page 354) is much shorter than the others for the same species. This represents a cultivated specimen (at the CSIRO Arboretum, Atherton) and may be interpreted as being somewhat aberrant compared with those seen in the field and on herbarium specimens, since flowers from the same plant have all the critical diagnostic features of *R. macrocarpa* given in Table 1.

Thick staminal scars (remnant filament bases) protrude from the staminal disc. These are more apparent on immature fruit (Lucas *et al.* 2019; Fig 2B1); in the mature fruit the scars resemble shallow pits in the disc.

Although all acrodromous species of *Rhodomyrtus* in Australia are currently being heavily impacted and threatened by Myrtle Rust, limited observations suggest that *R. verecunda* might not be susceptible to this pathogen. Species that were affected by Myrtle Rust, growing in the same area as *R. verecunda*, included: *Lindsayomyrtus racemoides* (Greves) Craven, *Rhodamnia sessiliflora* Benth. and *Rhodomyrtus effusa* Guymer. Further fieldwork is required to confirm this preliminary assessment. Of the other two non-acrodromous species, *R. psidioides* has been impacted severely by Myrtle Rust with some local populations experiencing complete destruction and, as a result, this species has been upgraded to Critically Endangered in both NSW and Queensland under respective state authorities (https://apps.des.qld.gov.au/species-search/details/?id=16290 and http://www.environment.gov.au/biodiversity/threatened/species/pubs/19162-conservation-advice-12122020.pdf), whilst *R. macrocarpa* is regarded as moderately susceptible (Makinson 2018).

Additional specimens seen: QUEENSLAND: Cook District: Daintree National Park, Mt Sorrow Track razorback, 4 km W of Cape Tribulation, 2 Dec 1997, *P. Forster PIF22005, R. Jago and R. Jensen* (BRI, CNS); Timber Reserve 165, Pieter Botte Logging Area, lower slopes of Mt Pieter Botte, 5 Aug 1997, *R. Russell 5* (CNS); head of Roaring Meg Creek–Cape Tribulation, May 1984, *M. Godwin 2583* (CNS); Daintree National Park, Noah Creek adjacent to Noah Island, 13 Jun 2016, *A. Ford AF6570, T. Hawkes and B. Gray* (BRI, CNS, NSW).

Key to the Species of *Rhodomyrtus* in Australia and their distribution within Queensland (modified from Snow and Cantley 2010).

1a. Leaf venation brochidodromous or eucamptodromous (not 3-veined) 2

1b. Leaf venation acrodromous (3-veined) 4

2a. Leaf venation brochidodromous, flowers solitary ..... ***R. verecunda*** (NQ)

2b. Leaf venation eucamptodromous, flowers usually in cymes to/or botryoids 3

3a. Placentation parietal, ovary 1-locular, seeds > 5mm diameter ..... ***R. macrocarpa*** (CQ, NQ, CYP)

3b. Placentation axile, ovary 2 or more locular, seeds < 5mm diameter ..... ***R. psidioides*** (SQ)

4a. Hairs on abaxial leaf surface whitish 5

4b. Hairs on abaxial leaf surface ferrugineous 6

5a. Indumentum of hypanthium and abaxial leaf surface sericeous with all hairs of similar length ..... ***R. canescens*** (NQ)

5b. Indumentum of hypanthium and abaxial leaf surface densely sericeous with additional longer villous hairs ..... ***R. sericea*** (NQ, CQ)

6a. Leaf base cordate to deeply obtuse; scandent, poorly formed shrubs ..... ***R. effusa*** (NQ)

6b. Leaf base cuneate to slightly obtuse; well-formed shrubs and small trees 7

7a. Ovules and seeds in 3–5 (rarely 7) longitudinal rows ..... ***R. trineura*** (CQ, NQ, CYP)

7b. Ovules and seeds in 7–14 longitudinal rows ..... ***R. pervagata*** (NQ)

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References

Cooper W (2004) *Fruits of the Australian tropical rainforest*. (Nokomis Editions, Melbourne)

Department of the Environment (2012) *Interim Biogeographic Regionalisation for Australia, Version 7*. http://www.environment.gov.au/land/nrs/science/ibra [accessed 23 June 2020]

Guymer GP (1991) Revision of the *Rhodomyrtus trineura* (F. Muell.) F. Muell. ex Benth. (Myrtaceae) species complex. *Austrobaileya* 3: 377–387. https://www.jstor.org/stable/41738778

IUCN Standards and Petitions Subcommittee (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Subcommittee. http://www.iucnredlist.org/documents/RedListGuidelines.pdf

Landrum LR, Kawasaki ML (1997) The genera of Myrtaceae in Brazil: an illustrated synoptic treatment and identification keys. *Brittonia* 49(4): 508–536. https://doi.org/10.2307/2807742

Landrum LR, Stevenson D (1986) Variability of Embryos in Subtribe Myrtinae (Myrtaceae). *Systematic Botany* 11(1): 155–162. https://doi.org/10.2307/2418954

Lucas EJ, Holst B, Sobral M, Mazine FF, Nic Lughadha EM, Barnes Proença CE, da Costa IR, Vasconcelos TNC (2019) A New Subtribal Classification of Tribe Myrteae (Myrtaceae). *Systematic Botany* 44(3): 560–569. https://doi.org/10.1600/036364419X15620113920608

Makinson RO (2018) Myrtle Rust reviewed: the impacts of the invasive pathogen *Austropuccinia psidii* on the Australian environment. Plant Biosecurity Cooperative Research Centre, Canberra. http://www.apbsf.org.au/wp-content/uploads/2018/11/Myrtle-Rust-reviewed-June-22-2018-web.pdf [accessed 5 August 2021]

Scott AJ (1978) A revision of *Rhodomyrtus* (Myrtaceae). *Kew Bulletin* 33: 311–329. https://doi.org/10.2307/4109586

Snow N, Guymer GP, Sawvel G (2003) Systematics of *Austromyrtus*, *Lenwebbia* and the Australian species of *Gossia* (Myrtaceae). *Systematic Botany Monographs* 65: 1–95. https://doi.org/10.2307/25027907

Snow N, Cantley J (2010) New species of *Uromyrtus* and *Rhodomyrtus* (Myrtaceae: Myrteae) from Kamiali Wildlife Management Area, Papua New Guinea, and an updated key to *Rhodomyrtus*. *Harvard Papers in Botany* 15: 63–70. https://www.jstor.org/stable/41761950

Snow N, McFadden J, Atwood JP (2008) Three new species of *Rhodomyrtus* (Myrtaceae) from Papua New Guinea. *Austrobaileya* 7: 691–706. https://www.biodiversitylibrary.org/item/281458#page/120/mode/1up

Snow N, McFadden J, Evans TM, Salywon AM, Wojciechowski MF, Wilson PG (2011) Morphological and molecular evidence of polyphyly in *Rhodomyrtus* (Myrtaceae: Myrteae). *Systematic Botany* 36: 390–404. https://doi.org/10.1600/036364411X569570

Wilson PG, O'Brien MM, Heslewood MM, Quinn CJ (2005) Relationships within Myrtaceae sensu lato based on a *matK* phylogeny. *Plant Systematics and Evolution* 251: 3–19. https://doi.org/10.1007/s00606-004-0162-y

Wilson PG (2011) Myrtaceae. Pp. 212–271 in Kubitzki, K. (ed.) *Families and Genera of Vascular Plants Vol. X. Flowering Plants. Eudicots: Sapindales, Cucurbitales, Myrtaceae*. (Springer-Verlag: Berlin) https://doi.org/10.1007/978-3-642-14397-7

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Molecular phylogenetic analysis of the *Prostanthera phylicifolia* (Lamiaceae) assemblage resolves relationships of the 'Critically Endangered' *P. gilesii* and other putative new species

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Abstract

Prostanthera gilesii Althofer ex. B.J.Conn & T.C.Wilson is a critically endangered species from the Central Tablelands of New South Wales. A conservation management strategy is currently underway for this species, whose phylogenetic affinities are not known. Morphologically, *P. gilesii* resembles *P. phylicifolia* F.Muell. and a population of uncertain identity from Evans Crown Nature Reserve in the Central Tablelands of New South Wales known as *P.* sp. Evans Crown (G.M.Taseski NSW1055966). The taxonomy of *P. phylicifolia,* however, is unclear. *Prostanthera phylicifolia* was described from populations in the Victorian Alps and Monaro; however, populations spanning from Victoria to southern Queensland have been variously identified as either *P. phylicifolia* or *P. scutellarioides* (R.Br.) Briq. despite substantial geographic disjunctions and morphological dissimilarity. To examine the relationship between populations identified as *P. phylicifolia, P. gilesii* and *P.* sp. Evans Crown, nuclear (external transcribed spacer, ETS) and chloroplast (*trn*H-*psb*A intergenic spacer) regions were sequenced and combined with an existing *Prostanthera* dataset and analysed with maximum-likelihood and Bayesian-inference methods. *Prostanthera gilesii* and *P.* sp. Evans Crown were recovered as sister taxa within a clade consisting of populations morphologically similar to the type of *P. phylicifolia* from the Victorian Alps and Snowy Mountains, Monaro and Southern Tablelands of New South Wales. Populations from northern New South Wales and southern Queensland identified as *P. phylicifolia* or *P. scutellarioides* were recovered as an assemblage of unrelated clades. The molecular phylogeny supports *P. gilesii* and *P. phylicifolia* as closely related as hypothesised based on morphology and supports *P.* sp. Evans Crown as a population which requires additional study to assess its taxonomic status.

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Introduction

Globally, isolated mountain masses and rock outcrops (e.g. shield volcanoes, inselbergs, monadnocks, tors) harbour a diverse range of narrowly endemic, highly specialised and threatened taxa (Porembski and Barthlott 2000; Michael *et al.* 2010). As these rocky outcrops often function as relictual ecosystems or refugia, they are particularly vulnerable to environmental threats such as climate change, land degradation, and altered fire regimes (Fitzsimons and Michael 2017; IUCN 2019; Selwood and Zimmer 2020). As an overwhelming body of evidence suggests that human-induced species loss is accelerating (Barnosky *et al.* 2011; Vos *et al.* 2014; Ceballos *et al.* 2015), there is an imperative to prioritise the understanding, documentation, and conservation of such fragmented biota.

Australian mint-bush, *Prostanthera* Labill., is the largest group of Australian Lamiaceae and many species have restricted ranges that are associated with isolated rock outcrops (Conn 1984, 1988; Conn and Wilson 2015). With striking floral displays and strongly aromatic leaves, various *Prostanthera* have horticultural, agricultural, and pharmaceutical value (Althofer 1978; Collins *et al.* 2014; Tang *et al.* 2017; Sadgrove *et al.* 2020). The Australian Plant Census (APC) currently recognises 100 species, 8 subspecies, and 18 standardised phrase-named species (APC 2021) in *Prostanthera*. Of the 100 accepted species, 19 are listed as "threatened" at a Commonwealth level (Department of Agriculture 1999, 2021) and 13 are listed as "threatened" in New South Wales (Government 2016; OEH 2021) representing almost a fifth of these species. One such species is the critically endangered *P. gilesii* Althofer ex. B.J.Conn & T.C.Wilson which is known from two small subpopulations on the shield volcano of Mount Canobolas State Conservation Area, south-west of Orange on the Central Tablelands of New South Wales (Figure 1A, Figure 2) (Conn and Wilson 2015). The species is the subject of targeted conservation research and management projects (OEH 2019; Scott and Auld 2020; Andrew *et al.* unpublished data) which includes population monitoring, genomic analysis, *ex situ* conservation and weed and pest management.

The phylogenetic relationship between *P. gilesii* and other *Prostanthera* is not known, which has impeded possible genomic conservation efforts. Althofer (1978) first recognised this species as *P.* sp. aff. *phylicifolia* (1978) and Conn and Wilson (2015) also identified a strong morphological similarity between *P. gilesii* and *P. phylicifolia* F.Muell. However, these similarities are difficult to reconcile as the taxonomic identity of *P. phylicifolia* has become unclear following changes implemented in Bentham's (1870) revision of the genus.

Prostanthera phylicifolia s. str. (Figure 1B, Figure 2) was described by Mueller (1858) from material collected from Mt Macfarlane (now Macfarlane's Lookout) near Omeo in northern Victoria and the "Maneroo" (present-day Monaro) region of New South Wales. Bentham's (1870) subsequent treatment of *P. phylicifolia* broadened its circumscription through citing specimens from the New England region, New South Wales, and the Glass House Mountains, Queensland, in addition to the Victorian type locality. Bentham's broad circumscription has caused taxonomic confusion, and populations from northern New South Wales and southern Queensland (Figure 2) have been variously assigned as either *P. phylicifolia* or *P. scutellarioides* (R.Br.) Briq. (Figure 1D), depending on herbaria curatorship. As an example, gatherings from these populations identified as *P. phylicifolia* (Figures 1E–F) sent as duplicates from the Queensland Herbarium (BRI) to the National Herbarium of New South Wales (NSW) have been reidentified at NSW as *P. scutellarioides*. While these populations share glabrous, narrow ovate leaves, floral morphology between northern and southern populations is largely variable (Figure 1). For example, southern populations share anthers with a distinctly elongated outgrowth of the connective tissue found between both pollen sacks (i.e. an anther appendage), while this appendage is reduced to absent in northern populations. Prior studies of floral types in *Prostanthera* (Wilson *et al.* 2017) suggest that such pronounced differences in floral type indicate that these groups are not closely related. Thus, further investigation is warranted across these populations.

Previous research into the systematics of *Prostanthera* included a sample from a southern population of *P. phylicifolia*, located at Deua National Park (Population 8, Figure 2), on the Southern Tablelands of New South Wales (Wilson *et al.* 2012; Conn *et al.* 2016). In these studies, this accession, and an accession of *P. scutellarioides* from Castlereagh Nature Reserve in the Sydney Basin were recovered as sister taxa, within a clade referred to as "Clade C". In Bentham's (1870) series classification, these two species were circumscribed within series *Convexae* Benth. While Wilson *et al.* (2012) revealed inconsistencies with Bentham's series and sectional classifications, they reported that most members of the *Convexae* were recovered within a well-supported "Clade C". Bentham's (1870) series *Convexae* encompasses species with small, shortly petiolate leaves with a convex–revolute margin and flowers that appear axillary. This may account for some confusion surrounding the identity of northern populations variously identified as either *P. phylicifolia* or *P. scutellarioides*. As none of these disjunct populations have been included in prior molecular studies of *Prostanthera*, their relationship with *P. phylicifolia* and *P. scutellarioides* is still unknown.

Fig. 1. Photographs of species and populations of *Prostanthera* investigated in this study. A = *P. gilesii*; B = *P. phylicifolia s. str.* (Tinderry); C = *P.* sp. Evans Crown; D = *P. scutellarioides s. str.* (Castlereagh Nature Reserve); E = *P. phylicifolia s. lat.* (Gibraltar Range National Park); F = *P.* sp. Minyon Falls. Images: T. C. Wilson (A); D. Indiarto (B); R. P. O'Donnell (C); G. M. Taseski (D); J. J. Bruhl (E); M. Colpus (F).

Another entity of uncertain identity that is morphologically similar to *P. phylicifolia s. str.* and *P. gilesii* is known from Evans Crown Nature Reserve on the Central Tablelands of New South Wales (Figure 1C, Figure 2). This entity (hereafter referred to as *P.* sp. Evans Crown (G.M.Taseski NSW1055966)) was first identified from herbarium material held at NSW while curating collections of *P. phylicifolia*. Collections from Evans Crown superficially resembled both *P. phylicifolia* and *P. gilesii* but appeared morphologically distinct on the basis of a dense indumentum of appressed retrorse hairs on all organs (vs ± glabrous to sparsely hairy, hairs antrorse for *P. phylicifolia* and *P. gilesii*), large elliptic prophylls (vs linear-terete for *P. phylicifolia* and narrow-elliptic for *P. gilesii*), and mericarps that are rugose and papillose with occasional long pilose hairs (vs reticulate, not distinctly papillose and glabrous for *P. phylicifolia*, mature mericarps not observed for *P. gilesii*). The phylogenetic affinities of *P.* sp. Evans Crown are also unknown. *Prostanthera gilesii* and *P.* sp. Evans Crown are most morphologically similar to *P. phylicifolia s. str.* and on this basis, we can posit that they are also members of "Clade C".

In this study, we used molecular evidence to determine the phylogenetic affinities of *P. gilesii* and *P.* sp. Evans Crown and investigate their relationship with populations variously determined as *P. phylicifolia* or *P. scutellarioides*. Molecular phylogenetic studies of *Prostanthera* using Sanger sequencing have allowed for the resolution of taxonomic issues between closely related taxa (Conn *et al.* 2013) and the separation of new species from morphologically similar accessions (Conn *et al.* 2016), but have also revealed the presence of species complexes (e.g. *P. howelliae* Blakely) that still require attention (Wilson *et al.* 2012). Here, we aim to extend our understanding of *P. phylicifolia* across its broader distribution, reconstruct the phylogenetic relationships of *P. gilesii, P. phylicifolia* and *P.* sp. Evans Crown, and test the monophyly of these taxa.

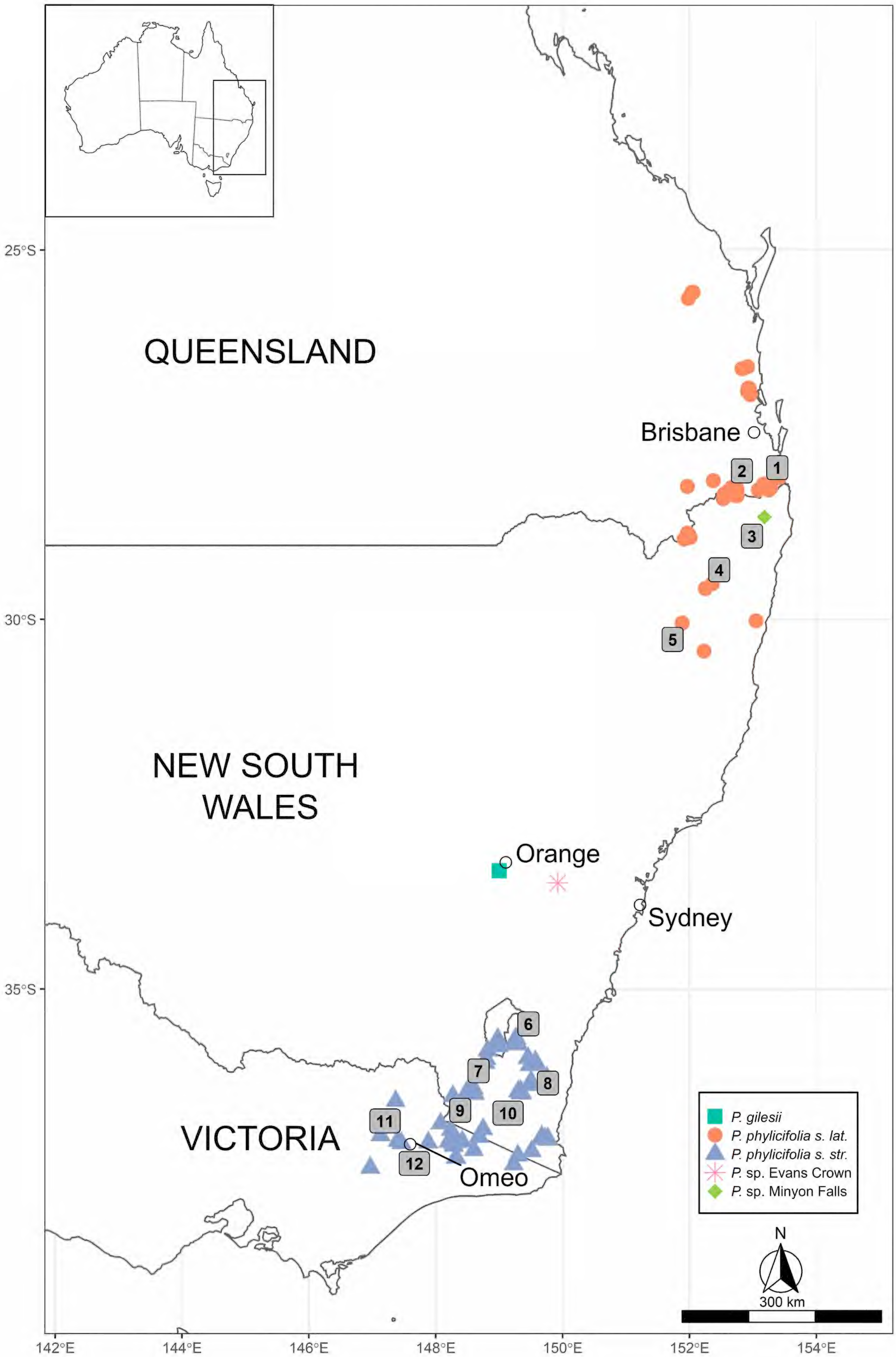

Fig. 2. Distribution map and sampled populations of *Prostanthera gilesii, P. phylicifolia s. lat., P. phylicifolia s. str., P.* sp. Evans Crown and *P.* sp. Minyon Falls based on AVH occurrence records (AVH 2021). 1 = Lamington NP; 2 = Mt. Barney NP; 3 = Minyon Falls; 4 = Gibraltar Range NP; 5 = Warra NP; 6 = Tinderry Ranges; 7 = Adaminaby; 8 = Deua NP; 9 = Kosciuszko NP; 10 = Dangelong NR; 11, 12 = Cobrunga.

Materials and Methods

Specimens

Leaf material for genetic analysis was sampled from material dried using silica gel or from herbarium material (Table 1). Samples of *P. gilesii* from the two known subpopulations at Towac Creek and The Walls, and two samples of *P.* sp. Evans Crown were used for analysis. Accessions representing 12 populations variously identified as *P. phylicifolia* or *P. scutellarioides* were included in our analyses. Populations sampled included five populations variously identified as *P. phylicifolia* or *P. scutellarioides* from northern New South Wales to southern Queensland (Figure 2, Populations 1–5), and seven populations considered to represent *P. phylicifolia s. str.* spanning from Victoria to the Southern Tablelands of New South Wales (Figure 2, Populations 6–12). As the northern accessions differ in their assignation between herbaria, they will be treated here as *P. phylicifolia s. lat.* following Bentham (1870). This includes one accession more recently assigned as *P.* sp. Minyon Falls (J.B.Williams *s.n.*, NE61356) I.Telford, which is maintained within the *P. phylicifolia* assemblage for simplicity (Figure 2, Population 3). An additional accession of *P. scutellarioides* from the Hunter Valley was sampled to test the northern limits of this species. Several specimens from Victoria identified as *P. phylicifolia* were observed as either glabrous or with a dense indumentum on all organs of entirely antrorse hairs, or occasionally retrorse hairs, which is consistent with Mueller's (1858, p.19) description of individuals of *P. phylicifolia* from the type locality as ranging from glabrous to velutinous ("glabra v. velutina"). Individual plants that are either entirely glabrous or densely hairy have previously been observed occurring within the same population (N.G. Walsh pers. comm. 2020). Leaf material from both glabrous and velutinous forms from the Cobungra region were collected for analysis from cultivated material held at the Royal Botanic Gardens Melbourne (MEL) and are here referred to as *P. phylicifolia* '*glabra*' and *P. phylicifolia* '*velutina*' *sensu* Mueller (1858) respectively.

Table 1. Accession details for specimens of *Prostanthera* and *Westringia* sampled for Sanger sequencing of nuclear (external transcribed spacer, ETS) and chloroplast (*trn*H-psbA intergenic spacer) markers in this study. Several accessions from previous studies were found to have been published with erroneous collection details that did not match those found on their respective herbarium voucher sheet or AVH database records. These samples are noted below and have been corrected to reflect their respective voucher sheets. GenBank accessions are given for each marker. P = *Prostanthera*; W = *Westringia*; CP = Conservation Park; NP = National Park; NR = Nature Reserve; SCA = State Conservation Area; SF = State Forest; N.S.W. = New South Wales; Qld = Queensland; S.A. = South Australia; Tas. = Tasmania; Vic. = Victoria; W.A. = Western Australia. New accessions for this study are indicated by bold text, ^ = previously published accessions with amended collection details.

Taxon	Locality	Voucher	Herbarium and accession #	ETS	*trn*H-*psb*A
P. albohirta	Mt Emerald, Qld	Ford 6174	CNS 010353.1	KU532856	KU563336
P. althoferi	Yalgoo, W.A.	Wilson 271	NSW 901182	KU532857	KU563337
P. althoferi	Kambalda East, W.A.	Wilson 360	NSW 902815	KU532858	KU563338
P. ammophila	Pinkawillinie CP, S.A.	Te 854	AD 232799	KU532859	KU563339
P. athertoniana	Kahlpahlim Rock, Qld	Ford 1835	NSW 1001033	KU532860	KU563340
P. baxteri	Ravensthorpe, W.A.	Wilson 380	NSW 845708	KU532861	KU563341
P. campbellii	East Pilbara, W.A.	Perkins WA101	PERTH 8461236	KU532862	KU563342
P. canaliculata	Toodyay, W.A.	Hislop *et al.* 178–7	PERTH 7433239	KU532863	KU563343
P. centralis^	Central Ranges, W.A.	Wilson 417	NSW 972502	KU532864	KU563344
P. clotteniana	Ravenshoe SF, Qld	Ford 5982	NSW 933508	KU532865	KU563345
P. densa	Port Stephens, N.S.W.	Wilson 37	NSW 789038	JX047677	KF145100
P. eckersleyana	Mt Marshall, W.A.	Horn 2508	PERTH 5686180	KU532866	KU563346
P. eungella	Eungella, Qld	McDonald 5131	NSW 452207	KU532867	KU563347
P. galbraithiae	Holey Plains, Vic.	Conn 5222	NSW 808463	JX047667	KU563348
***P. gilesii* (Towac)**	**Towac Creek, Mt. Canobolas SCA, N.S.W.**	**Bruhl 3602**	**NE 108967**	**OK524300**	**OK562349**
***P. gilesii* (Walls)**	**The Walls, Mt. Canobolas SCA, N.S.W.**	**Medd 7111**	-	**OK524301**	**OK562350**
P. granitica^	Warrumbungles NP, N.S.W.	Tuft 162	NSW 844192	JX047639	KU563349
P. howelliae^	Sackville, N.S.W.	Wilson 216	NSW 799701	JX047644	KU563350
P. laricoides	Yilgarn, W.A.	Edinger 6582	PERTH 7772394	KU532868	KU563351
P. lasianthos	Grampians NP, Vic.	Conn 5311	NSW 799716	KU532869	KU563352

Taxon	Locality	Voucher	Herbarium and accession #	ETS	*trn*H-*psb*A
P. lasianthos	Mt Field, Tas.	Henwood 864	NSW 836127	KU532871	KU563353
P. lasianthos	Mt Wilson, N.S.W.	Proft 3	NSW 105895	KU532870	KU563355
P. lasianthos	Blue Mountains NP, N.S.W.	Wilson 44	NSW 799707	JX047663	KU563354
P. marifolia	Sydney, N.S.W.	Conn 4380A	NSW 743858	JX047657	KF145108
P. mulliganensis	Mt Mulligan, Qld	Clarkson 5241	NSW 797165	KU532872	KU563356
P. nivea var. *induta*^	Warrumbungle Mountains, N.S.W.	Wilson 203	NSW 803949	JX047651	KU563357
P. nudula	Sentinel Hill, S.A.	Latz 24527	AD 240053	KU532873	KU563358
P. ovalifolia s. l.	Lamington NP, Qld	Forster PIF40534	AQ 836012	-	KU564718
P. ovalifolia s. l.	Whian Whian SCA, N.S.W.	Anon. AA 873108	NSW 4200941	JX047633	-
P. ovalifolia s. l.	Sherwood NR, N.S.W.	Wilson 139	NSW 799705	JX047622	-
P. patens	Blue Hills Range, W.A.	Markey & Dillon 3715	PERTH 7461267	KU532874	KU563359
***P. phylicifolia s. l.* (1)**	**Lamington NP, Qld**	**Beesley 1005**	**NSW 276830**	**OK524294**	**OK562342**
***P. phylicifolia s. l.* (2)**	**Mt. Barney NP, Qld**	**Mathieson 485**	**NSW 815397**	**OK524293**	**OK562343**
***P. phylicifolia s. l.* (4)**	**Gibraltar Range NP, N.S.W.**	**Taseski 961**	**NSW 1057452**	**OK524297**	**OK562346**
***P. phylicifolia s. l.* (5)**	**Warra NP, N.S.W.**	**Telford 13500**	**NE 101293**	**OK524292**	**OK562341**
***P. phylicifolia s. s.* (6)**	**Tinderry Ranges, N.S.W.**	**O'Donnell 61**	**NSW 1100407**	**OK524307**	**OK562356**
***P. phylicifolia s. s.* (7)**	**Adaminaby, N.S.W.**	**Medd 217100a1**	**NE 109825**	**OK524306**	**OK562355**
P. phylicifolia s. s. (8)	Deua NP, N.S.W.	Liney 2039	NSW 887109	JX047643	-
***P. phylicifolia s. s.* (9)**	**Kosciuszko NP, N.S.W.**	**Medd 217096a**	**NE 109821**	**OK524305**	**OK562354**
***P. phylicifolia s. s.* (10)**	**Dangelong NR, N.S.W.**	**Medd 217099b**	**NE 109826**	**OK524304**	**OK562353**
***P. phylicifolia s. s. 'velutina'* (11)**	**Cobrunga, Vic.**	**Walsh 8979**	**MEL 2470086**	**OK524302**	**OK562352**
***P. phylicifolia s. s. 'glabra'* (12)**	**Cobrunga, Vic.**	**Walsh 9013**	**MEL 2470120**	**OK524302**	**OK562351**
P. prostantheroides	Geeraning Rock, W.A.	Wilson 333	NSW 902203	KU532875	KU563360
P. ringens	Dubbo, N.S.W.	Wilson 153	NSW 844195	JX047605	KU563361
P. scutate	Northampton, W.A.	Porter 320	PERTH 7452268	KU532876	KU563362
P. scutellarioides^	Castlereagh NR, N.S.W.	Wilson 215	NSW 799702	JX047642	-
P. scutellarioides	**Myall River, N.S.W.**	**Bell s.n.**	**NSW 847837**	**OK524296**	**OK562345**
P. serpyllifolia subsp. *microphylla*	Breakaway Ridge NR, W.A.	Byrne 3929	PERTH 8274665	KU532877	KU563363
P. serpyllifolia subsp. *serpyllifolia*	Wickepin, W.A.	Pigott s.n.	PERTH 5098955	KU532878	KU563364
***P.* sp. Evans Crown**	**Evans Crown NR, N.S.W.**	**O'Donnell 28**	**NSW 1100357**	**OK524298**	**OK562347**
***P.* sp. Evans Crown**	**Evans Crown NR, N.S.W.**	**O'Donnell 29**	**NSW 1100369**	**OK524299**	**OK562348**
***P.* sp. Minyon Falls (3)**	**Nightcap NP, N.S.W.**	**Palsson 115**	**NE 105981**	**OK524295**	**OK562344**
P. tallowa	Kangaroo Valley, N.S.W.	Conn 5313	NSW 749547	JX047664	KF692284
P. tallowa	Morton NP, N.S.W.	Wilson 236	NSW 978753	KU532879	KU563365
P. verticillaris	Albany, W.A.	Wilson 388	NSW 903073	KU532880	KU563366
P. violacea	Blue Mountains NP, N.S.W.	Wilson 401	NSW 904871	KU532881	KU563367
W. longifolia	Goonoowigal SCA, N.S.W.	Wilson 458	NSW 977896	KU532882	KU563368
W. lucida	Kosciuszko NP, N.S.W.	Orme 600	NSW 619652	JX047601	-
W. senifolia	Mount Buffalo NP, Vic.	Wilson 159	NSW 799706	JX047600	-

Selection of molecular markers

Previous phylogenetic studies of *Prostanthera* have used the external transcribed spacer (ETS) region of nuclear ribosomal DNA, and the *ndh*F-*rpl*32, *trn*T-F, and *trn*H-*psb*A chloroplast regions (Wilson *et al.* 2012; Conn *et al.* 2013; Conn *et al.* 2016). Wilson *et al.* (2012) found that nuclear ETS data provided species-level resolution within *Prostanthera*, while the *ndh*F-*rpl*32 and *trn*T-F chloroplast regions provided poorer species-level resolution,

as they have in other genera within the Westringieae (Guerin 2008). Ensuant molecular phylogenetic studies within *Prostanthera* have continued to incorporate nuclear ETS data but have used the *trn*H-*psb*A chloroplast region in place of the *ndh*F-*rpl*32 and *trn*T-F chloroplast regions (Conn *et al.* 2013; Conn *et al.* 2016). Analysis of the *trn*H-*psb*A region by Conn *et al.* (2013) provided resolution at an interspecific level, but did not resolve relationships at the population scale. Conn *et al.* (2016) provided a phylogeny of the genus that exhibited moderate-to-strong support values; however, only the results of a concatenated (ETS + *trn*H-*psb*A) analysis were reported. It is unclear from the results of Conn *et al.* (2016) whether the *trn*H-*psb*A region itself provides robust results across *Prostanthera*, or whether the reasonable support values are more strongly influenced by the ETS dataset. This study presented an opportunity to assess the relative utility of the *trn*H-*psb*A region. To augment existing genetic studies within *Prostanthera* and to supplement our analyses using existing datasets, the nuclear ETS region and *trn*H-*psb*A chloroplast region were selected for use in this study.

Specimens sampled for Sanger sequencing

Sixteen samples of *Prostanthera* were newly sequenced for this study. Three samples of *Westringia* were used as an outgroup as they are also members of the Westringieae (Wilson *et al.* 2012; Conn *et al.* 2016). GenBank (Clark *et al.* 2016) accessions of the ETS and *trn*H-*psb*A regions used in previous studies of *Prostanthera* (Wilson *et al.* 2012; Conn *et al.* 2013; Conn *et al.* 2016) were combined with newly sequences from this study to provide a total nuclear dataset of 58 samples and a total chloroplast dataset of 53 samples (Table 1).

DNA extraction, amplification, and sequencing

DNA extractions, polymerase chain reaction (PCR) to amplify the selected regions, and sequencing were carried out by the Australian Genome Research Facility (AGRF) following methods outlined in Wilson *et al.* (2012), Conn *et al.* (2013) and Conn *et al.* (2016). Primers are listed in Table 2.

Table 2. Primers used for amplification of markers

Fragment	Primer Name	Direction	Sequence	Author(s)
ETS	ETS-PROS2	5′ to 3′	GCAGCGACGACATCCCAACC	(Baldwin and Markos 1998)
	18S-E	3′ to 5′	GCAGGATCAACCAGGTAGCA	(Wilson *et al.* 2012)
*trn*H-*psb*A	*psb*A	5′ to 3′	GTTATGCATGAACGTAATGCTC	(Tate and Simpson 2003)
	*trn*H^{GUG}	3′ to 5′	CGCGCATGCTGGTGGATTCACAATCC	(Sang *et al.* 1997)

Sequence assembly and phylogenetic analysis of Sanger data

Contigs were assembled using UGENE (Okonechnikov *et al.* 2012) and the "Map Sanger Reads to Reference" function. Reads were mapped using the default quality settings, with a trimming quality threshold of 30 and a minimum mapping similarity of 80%. For mapping the ETS region, an existing sequence of *P. phylicifolia* (JX047643.1) was used as a reference. For mapping the *trn*H-*psb*A chloroplast region, a sequence of *P. lasianthos* Labill. (KU563352.1) was used as a reference as there were no prior existing *trn*H-*psb*A sequences of *P. phylicifolia*. Chromatograms of forward and reverse reads were combined and then inspected visually to assess base call accuracy. Bases that were ambiguous due to overlapping base peaks were coded as polymorphic using IUPAC ambiguity codes.

Sequences were aligned in MEGA X (Kumar *et al.* 2018) using Clustal W and edited manually following visual inspection of the completed alignment. In addition to separate ETS and *trn*H-*psb*A datasets, a partitioned concatenated dataset was created from the two by using the "Concatenate Sequence Alignments" function in MEGA X. Substitution models were tested and implemented for each dataset (Table 3) using ModelFinder (Kalyaanamoorthy *et al.* 2017) as implemented in IQ-TREE (Nguyen *et al.* 2015).

Maximum-likelihood (ML) analyses were performed using IQ-TREE (Nguyen *et al.* 2015). Substitution models for each partition were unlinked (Chernomor *et al.* 2016). To estimate branch length and support, 1000 bootstrap replicates were calculated using ultrafast bootstrap approximation (UFBoot) (Hoang *et al.* 2018). For bootstrap replicates in partitioned analyses, a resampling strategy as outlined by Gadagkar *et al.* (2005) and Seo *et al.* (2005) was implemented to reduce the likelihood of false positives and incorrect branch support assignation. This method first resamples partitions and then sites within resampled partitions (Minh *et al.* 2021). Bootstrap values were considered strong if they provided ≥95% support, moderate from 80–94% and weak from 50–79%.

Bayesian analysis was conducted using MrBayes 3.2.7 (Ronquist *et al.* 2012). Substitution models for each partition were unlinked. For each analysis, two independent Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses were run. Four chains were used (one heated, three cold), running for 5 million generations, and sampled

every 1000th generation. A relative burn-in duration of 25% was used. Posterior probability (PP) values of 1 (Larget and Simon 1999) were considered as strong support, 0.9–0.99 as moderate support, and 0.8–0.89 as weak support.

The final best-scoring trees output from ML and Bayesian analyses were combined and visualised using TreeGraph 2 (Stöver and Müller 2010).

Results

Statistical data for each sequence alignment and their respective analyses are outlined in Table 3. Analysis of the concatenated ETS and *trn*H-*psb*A dataset recovered a better resolved tree with higher branch support than analysis of either region individually (Figure 3, Table 3).

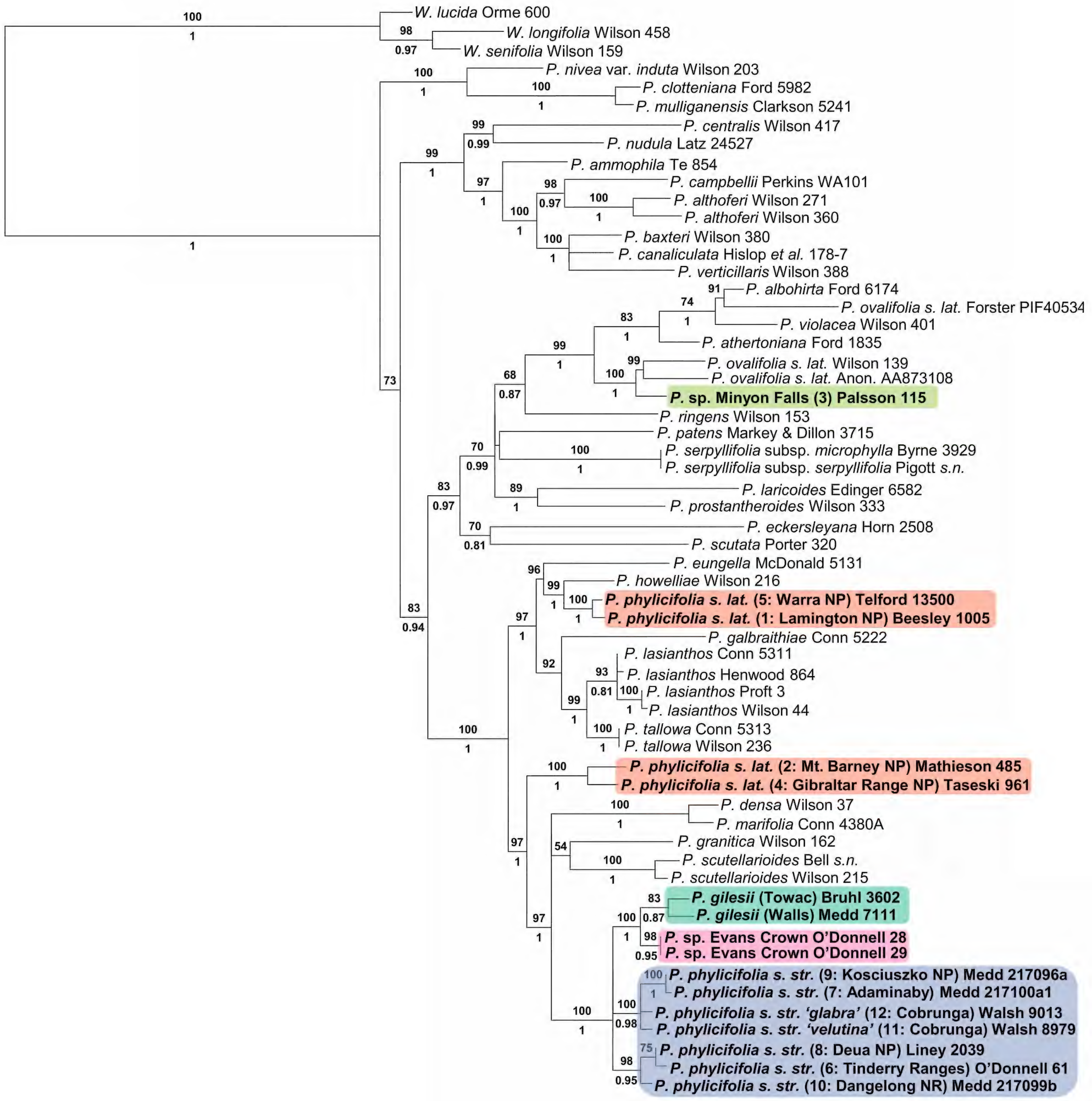

Fig. 3. Best scoring ML phylogram produced by IQ-TREE from analysis of the concatenated ETS and *trn*H-*psb*A sequence data for *Prostanthera* including three species of *Westringia* as outgroup representatives. Bayesian analysis posterior probabilities ≥0.8 from MrBayes and ML bootstrap values ≥50% are reported. *Prostanthera gilesii*, *P. phylicifolia s. str.*, *P. phylicifolia s. lat.*, *P.* sp. Minyon Falls and *P.* sp. Evans Crown are highlighted. Labels are species/phrase names, followed by primary collector and collection number. Labels for accessions of *P. phylicifolia* and *P. sp.* Minyon Falls include localities and population codes as outlined in Figure 2.

Table 3. Taxon information and statistics from Maximum Likelihood (ML) and Bayesian-inference analyses of nuclear (ETS) and chloroplast (*trn*H-*psb*A) markers**.**

Parameter	ETS	*trn*H-*psb*A	Concatenated
Total number of taxa	58	53	59
Total number of ingroup taxa	55	52	55
Total number of outgroup taxa	3	1	3
Aligned length	430	495	925
Parsimony-informative sites	188	44	Partitioned
Invariant sites	158	403	Partitioned
ModelFinder model	SYM + Γ	F81+I+Γ	Partitioned
Number of nodes resolved (IQ-TREE)	55	50	56
Number of nodes resolved (MrBayes)	46	20	49
Number of nodes resolved with BS ≥ 95%	34	7	36
Number of nodes resolved with PP = 1	20	3	29
% of nodes resolved with BS ≥ 95%	62	14	64
% of nodes resolved with PP = 1	43	15	59

Analysis of the concatenated dataset (Figure 3) recovered all samples of *P. phylicifolia* from southern New South Wales and Victoria (Populations 6–12, Figure 2) with *P. gilesii* and *P.* sp. Evans Crown in a well-supported clade (BS = 100%; PP = 1). This clade was recovered within a larger, strongly supported clade (BS = 97; PP = 1), sister to clades comprised of *P. granitica* Maiden & Betche*, P. scutellarioides, P. densa* A.A.Ham. and *P. marifolia* R.Br. *Prostanthera gilesii* and *P.* sp. Evans Crown were recovered together as sister taxa with strong support (BS = 100%; PP = 1). Both accessions of *P.* sp. Evans Crown were recovered as a distinct clade with moderate-to-strong support (BS = 98%; PP = 0.95), separate from *P. gilesii*. Both accessions of *P. gilesii* were recovered as a clade with weak-to-moderate support (BS = 83%; PP = 0.87). Specimens of *P. phylicifolia* formed two moderately-to-strongly supported clades. Accessions of *P. phylicifolia* from Cobrunga (including both glabrous and velutinous forms), Adaminaby, and Kosciuszko National Park formed a clade with moderate-to-strong support (BS = 100; PP = 0.98), and accessions from Tinderry, Deua National Park and Dangelong Nature Reserve were recovered as a clade with moderate-to-strong support (BS = 98%; PP = 0.95).

Accessions from populations from northern New South Wales and southern Queensland variously identified as *P. phylicifolia* or *P. scutellarioides* (Figure 2, Populations 1–5) were recovered in clades separated from the clade of accessions from southern New South Wales and Victoria. Specimens of *P. scutellarioides* from the Castlereagh type locality and from the Hunter Valley were recovered as a strongly supported clade (BS = 100%; PP = 1). Samples from Gibraltar Range National Park and Mt. Barney National Park were recovered together as a distinct, strongly supported clade (BS = 100%; PP = 1), sister to the clade comprised of *P. granitica, P. scutellarioides, P. densa, P. marifolia,* and the *P. gilesii-P. phylicifolia-P.* sp. Evans Crown clade. Samples from Warra National Park and Lamington National Park were recovered together in a strongly supported clade (BS = 100%; PP = 1) sister to *P. howelliae* within a strongly-supported clade (BS = 100%; PP = 1). This clade was recovered as a sister clade to *P. eungella* B.J.Conn & K.M.Proft. The accession of *P.* sp. Minyon Falls was recovered in a strongly supported clade (BS = 100%; PP = 1) with *P. ovalifolia* R.Br., sister to a clade with moderate-to-strong support (BS = 83%; PP = 1) containing *P. athertoniana* B.J.Conn & T.C.Wilson*, P. violacea* R.Br., and *P. albohirta* C.T.White.

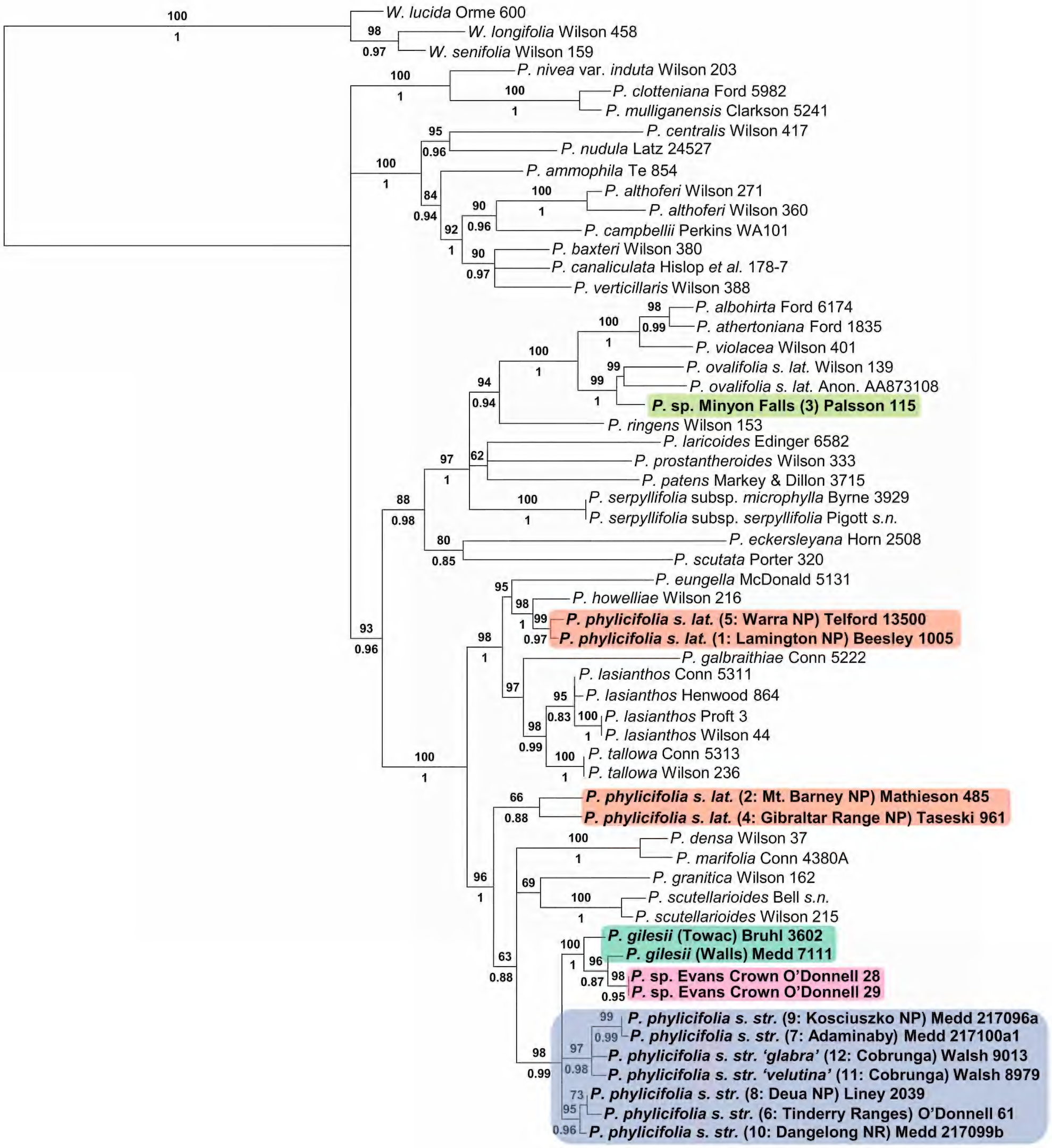

Fig. 4. Best scoring ML phylogram produced by IQ-TREE from analysis of nuclear ETS sequence data for *Prostanthera* including three species of *Westringia* as outgroup representatives. Bayesian analysis posterior probabilities ≥0.8 from MrBayes and ML bootstrap values ≥50% are reported. *Prostanthera gilesii*, *P. phylicifolia s. str.*, *P. phylicifolia s. lat.*, *P.* sp. Minyon Falls and *P.* sp. Evans Crown are highlighted. Labels are species/phrase names, followed by primary collector and collection number. Labels for accessions of *P. phylicifolia* and *P. sp.* Minyon Falls include localities and population codes as outlined in Figure 2.

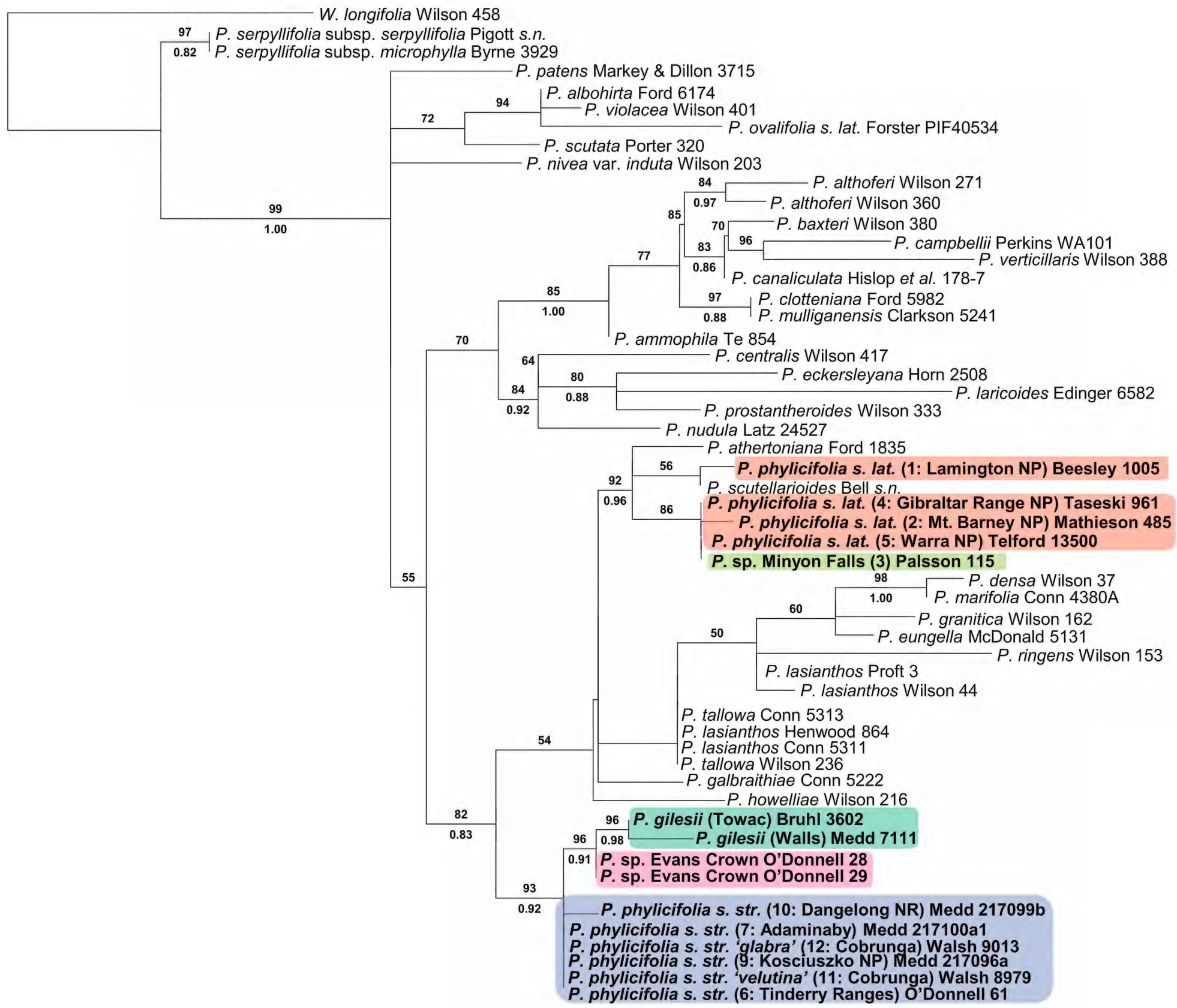

Fig. 5. Best scoring ML phylogram produced by IQ-TREE from analysis of chloroplast *trn*H-*psb*A sequence data for *Prostanthera* including one species of *Westringia* as an outgroup representative. Bayesian analysis posterior probabilities ≥0.8 from MrBayes and ML bootstrap values ≥50% are reported. *Prostanthera gilesii*, *P. phylicifolia s. str.*, *P. phylicifolia s. lat.*, *P.* sp. Minyon Falls and *P.* sp. Evans Crown are highlighted. Labels are species/phrase names, followed by primary collector and collection number. Labels for accessions of *P. phylicifolia* and *P. sp.* Minyon Falls include localities and population codes as outlined in Figure 2.

Analysis of the ETS region (Figure 4) recovered a tree not markedly different from that of the concatenated analysis, while analysis of the *trn*H-*psb*A region recovered a tree which differed substantially in topology and resolution (Figure 5). Analysis of the *trn*H-*psb*A region recovered all southern accessions of *P. phylicifolia.*, *P. gilesii* and *P.* sp. Evans Crown as a moderately supported clade (BS = 93%; PP = 0.92). Within this clade, *P. gilesii* and *P.* sp. Evans Crown were recovered as sister taxa with moderate-to-strong support (BS = 96%; PP = 0.91), sister to an unresolved polytomy consisting of all southern samples of *P. phylicifolia*. Both specimens of *P. gilesii* were recovered as a distinct clade with moderate-to-strong support (BS = 96%; PP = 0.98). This clade was recovered as sister to a larger, poorly-supported clade (BS = 54%; PP = N/A), which contained *P. howelliae, P. densa, P. marifolia, P. granitica, P. eungella, P. galbraithiae* B.J.Conn, *P. tallowa* B.J.Conn & T.C.Wilson, *P. lasianthos, P. athertoniana, P. scutellarioides,* and all northern samples variously identified as *P. phylicifolia* or *P. scutellarioides*. Northern samples identified as either *P. phylicifolia* or *P. scutellarioides* were recovered as a moderately-supported clade (BS = 92%; PP = 0.96) with *P. scutellarioides* and *P. athertoniana*. Relationships within this clade differed between ML and Bayesian analyses. Bayesian analyses recovered all northern accessions as a polytomy with weak support (PP = 0.82) distinct from *P. scutellarioides* and *P. athertoniana*. ML analyses recovered *P.* sp. Minyon Falls and accessions from Warra National Park, Mt. Barney National Park and Gibraltar Range National Park as a moderately-supported polytomy (BS = 86%), while the accession from Lamington National Park was recovered in a poorly-supported clade with *P. scutellarioides* (BS = 56%).

Discussion

The results of this study support a close relationship between *P. gilesii*, *P. phylicifolia s. str.* and *P.* sp. Evans Crown and their placement within "Clade C". Furthermore, our results highlight that *P. phylicifolia* as currently circumscribed is not monophyletic. Morphologically and geographically disparate populations variously identified as *P. phylicifolia* or *P. scutellarioides* demonstrably represent more than two distinct taxa.

All southern populations of *P. phylicifolia* from Victoria through to south of Canberra share a cohesive morphology characterised by white corollas with porrect adaxial lobes, purple and yellow throat markings, distinctly elongated anther appendages that either match or exceed the length of the anther cell, and leaves that are narrow-ovate to oblong with an obtuse apex. The morphology and locality shared by these populations is congruent with that identified for *P. phylicifolia* in Mueller's (1858) protologue and they are shown here to be closely related, although recovered across two distinct clades that each have a distinct geographic distribution. Populations occurring along the Victorian Alps and Snowy Mountains form a 'western' clade, while populations from the Tinderry Mountains south to Dangelong Nature Reserve form an 'eastern' clade. The biogeographic pattern examined here might be of further use to studies examining how topography and orogeny may have influenced speciation processes in south-eastern Australia. Analyses here did not support substantive genetic differentiation between glabrous and velutinous individuals and as both forms have been found to grow adjacently within populations, recognition of distinct varieties is unwarranted. This result highlights that caution must be taken when delimiting species of *Prostanthera* based solely on differences in indumentum. The contrasting levels of resolution between phylogenies recovered here indicate that further close study of this group at the population level is necessary to assess the extent of molecular and morphological divergence between the western and eastern clades As the taxonomic status of these clades is still uncertain, we have elected to refrain from designating a lectotype for *P. phylicifolia s. str.* here. For the meantime, application of *P. phylicifolia s. str.* should be restricted to these southern populations, excluding all populations from northern New South Wales and southern Queensland.

Similar to *P. phylicifolia s. str.*, *P. gilesii* and *P.* sp. Evans Crown are compact shrubs that exhibit leaves that are narrow-ovate to oblong with recurved margins and an obtuse apex, flowers with white corollas, purple and yellow throat markings, and anther appendages that either match or exceed the length of the anther cell. While *P. gilesii* and *P.* sp. Evans Crown are consistently recovered as sister taxa, they are separated by over 120 km and occupy different substrates (basalt for *P. gilesii* vs. granite for *P.* sp. Evans Crown) (Conn and Wilson 2015). On the basis of these differences, there is evidence to suggest a lack of contemporary gene flow between them. Nevertheless, it is unclear from the results presented here whether *P. gilesii* and *P.* sp. Evans Crown represent distinct taxa independent from *P. phylicifolia s. str.* If evidence for contemporary gene flow between the three taxa can be presented, it might follow that *P. gilesii* and *P.* sp. Evans Crown should be subsumed into *P. phylicifolia*. However, if further study were to unequivocally demonstrate that each taxon represents an independently evolving lineage, *P. gilesii* would retain its critically endangered status, its range would be restricted to the two known subpopulations within one catchment, and *P.* sp. Evans Crown would merit recognition at the specific rank. If *P.* sp. Evans Crown is a distinct species, it is likely that it would be of critical conservation concern on the basis of its restricted distribution and small population size. Within *Prostanthera*, a close study of the sister species *P. densa* and *P. marifolia* (Conn *et al.* 2013) demonstrated clear boundaries between the two species by incorporating population-level genetic data and statistical tests of morphological variation. Similar integrative taxonomic studies are required here to elucidate the molecular and morphological relationships and boundaries between *P. phylicifolia s. str.*, *P. gilesii* and *P.* sp. Evans Crown before firm taxonomic and conservation conclusions can be made.

Fig. 6. Photographs of *P.* sp. Minyon Falls and *P. ovalifolia s. lat*. A = *P.* sp. Minyon Falls; B = *P. ovalifolia s. lat.* (Nightcap National Park), demonstrating similarities in floral morphology and differences in vegetative morphology. Images: M. Colpus (A); J. J. Bruhl (B).

Populations that have been previously assigned as *P. phylicifolia s. lat.* or *P. scutellarioides* from northern New South Wales and southern Queensland are readily morphologically distinguishable from southern populations deemed as *P. phylicifolia s. str.* and molecular evidence here corroborates this distinction. These populations represent an assemblage of taxa that are only broadly related to *P. phylicifolia s. str.* or *P. scutellarioides*, several of which are possibly undescribed. While molecular data indicate that several putative species may be present, it is difficult to distinguish clear morphological discontinuities between them. Superficial variation between putative entities in this group can be seen in lamina length and width, however it is unclear whether this variation in vegetative traits is simply the result of phenotypic plasticity. This group requires a rigorous assessment of genetic and morphological variation to ascertain an accurate understanding of extant diversity.

Prostanthera sp. Minyon Falls (Figure 6A) bears no strong resemblance to species it was recovered with in nuclear and concatenated analyses (Figure 6B), but most closely resembles species it was recovered with in chloroplast analyses (Figures 1D, E) *Prostanthera* sp. Minyon Falls most closely resembles accessions collected on the Tweed Volcano, namely the Lamington National Park accession which was recovered as sister to the Warra National Park accession within a clade containing *P. howelliae* and *P. eungella* in concatenated and nuclear analyses. This taxon has linear leaves with revolute margins, apices that are acute to apiculate and flowers that are axillary, similar to other taxa recovered in "Clade C" after Wilson *et al.* (2012). Analysis of the chloroplast dataset recovered this accession in a clade including other "Clade C" taxa, as hypothesised based on morphological characters. In contrast, nuclear and concatenated analyses recovered this accession as sister to *P. ovalifolia* (Figure 6B)—a species previously recovered within "Clade J" after Wilson *et al.* (2012).

This pattern of results is repeated in our analyses in *P. athertoniana,* a narrowly restricted species from north-eastern Queensland. Of the accessions identified as *P. ovalifolia,* one was collected from Whian Whian State Conservation Area, which is adjacent to Minyon Falls. Similar to *P. phylicifolia*, *P. ovalifolia* is another species with contentious taxonomy, and accessions from this locality are variously identified as *P. ovalifolia* or *P. lanceolata* Domin. Recent genetic studies of this group have shown accessions considered under either name to be firmly placed within "Clade J" (Palsson *et al.* unpublished data). Like other members of "Clade J", these accessions can be characterised by leaves that are narrow-ovate to ovate with entire to minutely toothed margins and flowers in a terminal botryoid (Wilson *et al.* 2012). While *P.* sp. Minyon Falls can be readily distinguished from these accessions on the basis of leaf morphology and inflorescence type, they all share

mauve–purple flowers with corollas that are less strongly zygomorphic, lateral lobes directed outward and anther appendages that are reduced to absent (Wilson *et al.* 2012, 2017) (Figures 6A, B). This combination of floral characters corresponds with a generalist pollination syndrome found to be more frequently visited by an unspecialised pollinator assemblage consisting of flies and beetles (Wilson *et al.* 2017). This suggests that sympatric species exhibiting this floral type are likely to share pollen if they flower synchronously.

The different placement of *P.* sp. Minyon Falls in nuclear and chloroplast regions suggests that hybridisation may have occurred between sympatric species of *Prostanthera*. Cytonuclear discordance is commonly observed in phylogenetic studies and is often attributed to either incomplete lineage sorting or hybridisation (Lee-Yaw *et al.* 2019; Nge *et al.* 2021). Hybridisation in *Prostanthera* is documented in cultivation in the horticultural literature (Althofer 1978) and has been hypothesised to explain aberrant collections and populations (Conn 1998); however, there has been no genetic evidence to date to substantiate these hypotheses. If hybridisation can be confirmed, this study may represent the first genetic evidence of hybridisation in *Prostanthera* in wild populations. While it is unclear whether the cytonuclear discordance observed here is the result of a recent hybridisation event, ancestral introgression, or incomplete lineage sorting, we have identified strong candidate taxa to investigate this phenomenon further. As cytonuclear discordance was observed across multiple taxa in this study, it is probable that more densely sampled phylogenies of *Prostanthera* would reveal further instances of this phenomenon. If hybridisation is shown to be responsible for this pattern, future studies of *Prostanthera* must consider and test for this in order to avoid taxonomic over-inflation. Genomic technologies are now readily accessible and have demonstrated their efficacy in resolving questions of hybridisation and admixture (Sansaloni *et al.* 2010; Steane *et al.* 2011; Rutherford *et al.* 2018; Alwadani *et al.* 2019; Collins *et al.* 2021). Population-scale studies that incorporate genomic data from *P.* sp. Minyon Falls and other species found within the region may be able to elucidate the affinities of this taxon and the genetic processes at play.

The results of this study and other studies of *Prostanthera* (Conn *et al.* 2013; Conn *et al.* 2016) indicate that the *trn*H-*psb*A region provides poor resolution within the genus, which casts further doubt on the utility of the region as a DNA barcode. Similar to previous molecular studies of *Prostanthera* (Conn *et al.* 2013; Conn *et al.* 2016), the *trn*H-*psb*A chloroplast marker demonstrated substantially less resolution than the ETS nuclear marker (Figs. 4, 5, Table 3). The region had been originally identified as a good candidate for use as an efficient DNA barcode, with some success with its implementation (Pang *et al.* 2012; Hoveka *et al.* 2016; Loera-Sánchez *et al.* 2020). Previous studies stressed that the region should be analysed in combination with at least one to three additional chloroplast regions and a rapidly evolving nuclear region (e.g. ITS, ETS). When compared with other variable chloroplast regions, the *trn*H-*psb*A region has been shown to yield results that are not markedly different from comparable regions and caution has been advised in its use for barcoding purposes (Byrne and Hankinson 2012). Chase *et al.* (2007) noted that the region is highly variable in length (<300bp to >1000bp) even between closely related taxa, and exhibits high rates of insertions and deletions, making alignments difficult and prone to error. Other studies incorporating analysis of the region have demonstrated unresolved results like those obtained in this study (Whitlock *et al.* 2010; Singh *et al.* 2012; Chandrasekara *et al.* 2021). In a study of some species of Gentianaceae, the region was found to exhibit intraspecific inversions, potentially resulting in overestimation of divergence in conspecific taxa (Whitlock *et al.* 2010; Chandrasekara *et al.* 2021). Continued use of this region in studies of *Prostanthera* is unlikely to yield robust results.

Conclusion

Molecular evidence here has clarified the identity of *P. phylicifolia s. str.* Our results indicate that application of the name *P. phylicifolia* should be restricted to populations south of Canberra through to Victoria. These populations are unrelated to morphologically and geographically disparate northern populations variously identified as *P. phylicifolia* or *P. scutellarioides*. Rigorous morphological and genetic assessment will be required before taxonomic conclusions can be made.

In this study we have identified *P. phylicifolia s. str.* and *P.* sp. Evans Crown as close relatives of the critically endangered *P. gilesii*. *Prostanthera* sp. Evans Crown is most closely related to *P. gilesii,* and it is possible that it represents a new species of *Prostanthera*. As phylogenies estimated here exhibited variable topologies and support levels, we recommend further analysis of a more comprehensive sample set at the population scale, using high-throughput technologies that have been shown to be effective in resolving questions of historical gene flow and genetic divergence between putative taxa (Sansaloni *et al.* 2010; Steane *et al.* 2011; Collins *et al.* 2021; Joyce *et al.* 2021).

Our results highlight how broad species concepts and unresolved taxonomic issues have impeded an accurate understanding of diversity within *Prostanthera*. *Prostanthera* is already the most speciose Australian genus of Lamiaceae, and we have shown that it is highly likely that the genus is far more diverse than currently recognised.

Furthermore, we have demonstrated that *Prostanthera* is subject to confounding evolutionary processes such as incomplete lineage sorting and hybridisation. Tools better equipped to handle complex situations such as these will be crucial to achieving a clearer understanding of the evolutionary history of *Prostanthera*.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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References

Althofer GW (Ed. WH Payne) (1978) '*Cradle of incense: The story of Australian Prostanthera*.' (Society for Growing Australian Plants: Picnic Point, NSW)

Alwadani KG, Janes JK, Andrew RL (2019) Chloroplast genome analysis of box-ironbark *Eucalyptus*. *Molecular Phylogenetics and Evolution* **136**, 76–86. https://doi.org/10.1016/j.ympev.2019.04.001

APC (2021) 'APC: *Prostanthera*.' Available at https://biodiversity.org.au/nsl/services/rest/treeElement/51411005/51380123 [Accessed 09/04/2021].

AVH (2021) 'Australia's Virtual Herbarium, distribution map of *Prostanthera phylicifolia, P. gilesii* and *P.* sp. Evans Crown.' Available at http://avh.ala.org.au/ [Accessed 25/04/2021].

Baldwin BG, Markos S (1998) Phylogenetic Utility of the External Transcribed Spacer (ETS) of 18S–26S rDNA: Congruence of ETS and ITS trees of *Calycadenia* (Compositae). *Molecular Phylogenetics and Evolution* **10**, 449–463. https://doi.org/10.1006/mpev.1998.0545

Barnosky A, Matzke N, Tomiya S, Wogan G, Swartz B, Quental T, Marshall C, McGuire J, Lindsey E, Maguire KC, Mersey B, Ferrer E (2011) Has the earth's sixth mass extinction already arrived? *Nature* **471**, 51–57. https://doi.org/10.1038/nature09678

Bentham G (1870) Labiatae. In '*Flora Australiensis*.' Vol. 5 pp. 70–137. (Reeve: London)

Byrne M, Hankinson M (2012) Testing the variability of chloroplast sequences for plant phylogeography. *Australian Journal of Botany* **60**, 569–574. https://doi.org/10.1071/BT12146

Ceballos G, Ehrlich P, Barnosky A, Garcia A, Pringle R, Palmer T (2015) Accelerated Modern Human-Induced Species Losses: Entering the Sixth Mass Extinction. *Science Advances* **1**, e1400253. https://doi.org/10.1126/sciadv.1400253

Chandrasekara CHWMRB, Naranpanawa DNU, Bandusekara BS, Pushpakumara DKNG, Wijesundera DSA, Bandaranayake PCG (2021) Universal barcoding regions, *rbc*L, *mat*K and *trn*H-*psb*A do not discriminate *Cinnamomum* species in Sri Lanka. *PLOS ONE* **16**, e0245592. https://doi.org/10.1371/journal.pone.0245592

Chase MW, Cowan RS, Hollingsworth PM, van den Berg C, Madriñán S, Petersen G, Seberg O, Jørgsensen T, Cameron KM, Carine M, Pedersen N, Hedderson TAJ, Conrad F, Salazar GA, Richardson JE, Hollingsworth ML, Barraclough TG, Kelly L, Wilkinson M (2007) A proposal for a standardised protocol to barcode all land plants. *Taxon* **56**, 295–299. https://doi.org/10.1002/tax.562004

Chernomor O, von Haeseler A, Minh BQ (2016) Terrace Aware Data Structure for Phylogenomic Inference from Supermatrices. *Systematic Biology* **65**, 997–1008. https://doi.org/10.1093/sysbio/syw037

Clark K, Karsch-Mizrachi I, Lipman DJ, Ostell J, Sayers EW (2016) GenBank. *Nucleic Acids Research* **44**, D67–D72. https://doi.org/10.1093/nar/gkv1276

Collins TL, Bruhl JJ, Schmidt-Lebuhn A, Telford IRH, Andrew RL (2021) Tracing the origins of hybrids through history: monstrous cultivars and Napoléon Bonaparte's exiled paper daisies (Asteraceae; Gnaphalieae). *Botanical Journal of the Linnean Society* **44**, 277–289. https://doi.org/10.1093/botlinnean/boab020

Collins TL, Jones GL, Sadgrove NJ (2014) Volatiles from the rare Australian desert plant *Prostanthera centralis* B.J.Conn (Lamiaceae): Chemical composition and antimicrobial activity. *Agriculture* **4**, 308–316. https://doi.org/10.3390/agriculture4040308

Colpus M (2020) '*Prostanthera scutellarioides*.' Available at https://www.inaturalist.org/observations/58013471 [Accessed 27/07/2021].

Conn BJ (1984) A taxonomic revision of *Prostanthera* Labill. section *Klanderia* (F.v. Muell) Benth. (Labiatae). *Journal of the Adelaide Botanic Gardens* **6**, 207–348. https://data.environment.sa.gov.au/Content/Publications/JABG06P207_Conn.pdf

Conn BJ (1988) A taxonomic revision of *Prostanthera* Labill. section *Prostanthera* (Labiatae). 1. The species of the Northern Territory, South Australia and Western Australia. *Nuytsia* **6**, 351–411. https://www.biodiversitylibrary.org/item/223970#page/79/mode/1up

Conn BJ (1998) Contributions to the systematics of *Prostanthera* (Labiatae) in south-eastern Australia. *Telopea* **7**, 319–332. http://dx.doi.org/10.7751/telopea19982003

Conn BJ, Henwood MJ, Proft K, Wilson TC (2016) Molecular phylogenetics reveals a new species of *Prostanthera* from tropical Queensland with links to more southerly taxa. *Telopea* **19**, 13–22. http://dx.doi.org/10.7751/telopea10037

Conn BJ, Wilson TC (2015) Two new species of *Prostanthera* (Lamiaceae) in New South Wales. *Telopea* **18**, 463–474. http://dx.doi.org/10.7751/telopea9164

Conn BJ, Wilson TC, Henwood MJ, Proft K (2013) Circumscription and phylogenetic relationships of *Prostanthera densa* and *P. marifolia* (Lamiaceae). *Telopea* **15**, 149–164. http://dx.doi.org/10.7751/telopea2013019

Department of Agriculture, Water and the Environment 1999. Environment Protection and Biodiversity Conservation Act 1999. https://www.awe.gov.au/environment/epbc

Department of Agriculture, Water and the Environment (2021) 'EPBC Act List of Threatened Flora.' Available at https://www.environment.gov.au/cgi-bin/sprat/public/publicthreatenedlist.pl?wanted=flora [Accessed 08/04/2021].

Fitzsimons JA, Michael DR (2017) Rocky outcrops: A hard road in the conservation of critical habitats. *Biological Conservation* **211**, 36–44. https://doi.org/10.1016/j.biocon.2016.11.019

Gadagkar SR, Rosenberg MS, Kumar S (2005) Inferring species phylogenies from multiple genes: Concatenated sequence tree versus consensus gene tree. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* **304B**, 64–74. https://doi.org/10.1002/jez.b.21026

Government NSW, 2016. Biodiversity Conservation Act 2016.

Guerin GR (2008) Evidence for polyphyly in *Hemigenia* and *Microcorys* (Lamiaceae: Westringieae). *Australian Systematic Botany* **21**, 313–325. https://doi.org/10.1071/SB08008

Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: Improving the Ultrafast Bootstrap Approximation. *Molecular Biology and Evolution* **35**, 518–522. https://doi.org/10.1093/molbev/msx281

Hoveka LN, van der Bank M, Boatwright JS, Bezeng BS, Yessoufou K (2016) The noncoding *trn*H-*psb*A spacer, as an effective DNA barcode for aquatic freshwater plants, reveals prohibited invasive species in aquarium trade in South Africa. *South African Journal of Botany* **102**, 208–216. https://doi.org/10.1016/j.sajb.2015.06.014

IUCN (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Prepared by the Standards and Petitions Committee of the IUCN Species Survival Commission. Available at http://www.iucnredlist.org/documents/RedListGuidelines.pdf [Accessed 25/3/2020].

Joyce EM, Pannell CM, Rossetto M, Yap J-YS, Thiele KR, Wilson PD, Crayn DM (2021) Molecular phylogeography reveals two geographically and temporally separated floristic exchange tracks between Southeast Asia and northern Australia. *Journal of Biogeography* **48**, 1213–1227. https://doi.org/10.1111/jbi.14072

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* **14**, 587–589. https://doi.org/10.1038/nmeth.4285

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. *Molecular Biology and Evolution* **35**, 1547–1549. https://doi.org/10.1093/molbev/msy096

Larget B, Simon DL (1999) Markov Chasin Monte Carlo algorithms for the Bayesian analysis of phylogenetic trees. *Molecular Biology and Evolution* **16**, 750–759. https://doi.org/10.1093/oxfordjournals.molbev.a026160

Lee-Yaw JA, Grassa CJ, Joly S, Andrew RL, Rieseberg LH (2019) An evaluation of alternative explanations for widespread cytonuclear discordance in annual sunflowers (*Helianthus*). *New Phytologist* **221**, 515–526. https://doi.org/10.1111/nph.15386

Loera-Sánchez M, Studer B, Kölliker R (2020) DNA barcode *trn*H-*psb*A is a promising candidate for efficient identification of forage legumes and grasses. *BMC Research Notes* **13**, 35. https://doi.org/10.1186/s13104-020-4897-5

Michael DR, Lindenmayer DB, Cunningham RB (2010) Managing rock outcrops to improve biodiversity conservation in Australian agricultural landscapes. *Ecological Management & Restoration* **11**, 43–50. https://doi.org/10.1111/j.1442-8903.2010.00512.x

Minh BQ, Lanfear R, Trifinopoulos J, Schrempf D, Schmidt HA (2021) IQ-TREE version 2.1.2: Tutorials and Manual Phylogenomic software by maximum likelihood. Available at http://www.iqtree.org/doc/iqtree-doc.pdf

Mueller FJH von (1858) *Prostanthera phylicifolia*. In '*Fragmenta Phytographiae Australiae*.' Vol. 1 pp. 19. (Auctoritate Gubern: Melbourne) https://www.biodiversitylibrary.org/item/7218#page/21/mode/1up

Nge FJ, Biffin E, Thiele KR, Waycott M (2021) Reticulate evolution, ancient chloroplast haplotypes, and rapid radiation of the Australian plant genus *Adenanthos* (Proteaceae). *Frontiers in Ecology and Evolution* **8**, 616741. https://doi.org/10.3389/fevo.2020.616741

Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* **32**, 268–274. https://doi.org/10.1093/molbev/msu300

OEH (2019) Saving Our Species *Prostanthera gilesii* 2018–2019 annual report card. Available at https://www.environment.nsw.gov.au/-/media/OEH/Corporate-Site/Documents/Animals-and-plants/Threatened-species/Report-cards/2018-2019/02-site-managed-flora/prostanthera-gilesii-2018-19.PDF

OEH (2021) 'Threatened biodiversity profile search.' Available at https://www.environment.nsw.gov.au/threatenedSpeciesApp/ [Accessed 08/04/2021].

Okonechnikov K, Golosova O, Fursov M (2012) Unipro UGENE: a unified bioinformatics toolkit. *Bioinformatics* **28**, 1166–1167. https://doi.org/10.1093/bioinformatics/bts091

Pang X, Liu C, Shi L, Liu R, Liang D, Li H, Cherny SS, Chen S (2012) Utility of the *trn*H-*psb*A intergenic spacer region and its combinations as plant DNA barcodes: a meta-analysis. *PLOS ONE* **7**, e48833. https://doi.org/10.1371/journal.pone.0048833

Porembski S, Barthlott W (2000) '*Inselbergs. Biotic diversity of isolated rock outcrops in tropical and temperate regions.*' (Springer-Verlag: Heidelberg, Germany)

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**, 539–542. https://doi.org/10.1093/sysbio/sys029

Rutherford S, Rossetto M, Bragg JG, McPherson H, Benson D, Bonser SP, Wilson PG (2018) Speciation in the presence of gene flow: population genomics of closely related and diverging *Eucalyptus* species. *Heredity* **121**, 126–141. https://doi.org/10.1038/s41437-018-0073-2

Sadgrove NJ, Padilla-González GF, Telford IRH, Greatrex BW, Jones GL, Andrew R, Bruhl JJ, Langat MK, Melnikovova I, Fernandez-Cusimamani E (2020) *Prostanthera* (Lamiaceae) as a 'Cradle of incense': Chemophenetics of rare essential oils from both new and forgotten Australian 'Mint Bush' species. *Plants* **9**, 11. https://doi.org/10.3390/plants9111570

Sang T, Crawford DJ, Stuessy TF (1997) Chloroplast DNA phylogeny, reticulate evolution, and biogeography of *Paeonia* (Paeoniaceae). *American Journal of Botany* **84**, 1120–1136. https://doi.org/10.2307/2446155

Sansaloni CP, Petroli CD, Carling J, Hudson CJ, Steane DA, Myburg AA, Grattapaglia D, Vaillancourt RE, Kilian A (2010) A high-density Diversity Arrays Technology (DArT) microarray for genome-wide genotyping in *Eucalyptus*. *Plant Methods* **6**, 6–16. https://doi.org/10.1186/1746-4811-6-16

Scott J, Auld TD (2020) Conservation assessment of *Prostanthera gilesii* Althofer ex B.J.Conn & T.C.Wilson (family Lamiaceae) NSW Department of Planning, Industry and Environment. Available at https://www.environment.gov.au/system/files/consultations/4264ba54-69fc-481f-afdc-595842e69006/files/conservation-assessment-prostanthera-gilesii.pdf

Selwood K, Zimmer H (2020) Refuges for biodiversity conservation: A review of the evidence. *Biological Conservation* **245**, 108502. https://doi.org/10.1016/j.biocon.2020.108502

Seo T-K, Kishino H, Thorne JL (2005) Incorporating gene-specific variation when inferring and evaluating optimal evolutionary tree topologies from multilocus sequence data. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 4436–4441. https://doi.org/10.1073/pnas.0408313102

Singh HK, Parveen I, Raghuvanshi S, Babbar SB (2012) The loci recommended as universal barcodes for plants on the basis of floristic studies may not work with congeneric species as exemplified by DNA barcoding of *Dendrobium* species. *BMC Research Notes* **5**, 42. https://doi.org/10.1186/1756-0500-5-42

Steane DA, Nicolle D, Sansaloni CP, Petroli CD, Carling J, Kilian A, Myburg AA, Grattapaglia D, Vaillancourt RE (2011) Population genetic analysis and phylogeny reconstruction in *Eucalyptus* (Myrtaceae) using high-throughput, genome-wide genotyping. *Molecular Phylogenetics and Evolution* **59**, 206–224. https://doi.org/10.1016/j.ympev.2011.02.003

Stöver BC, Müller KF (2010) TreeGraph 2: Combining and visualizing evidence from different phylogenetic analyses. *BMC Bioinformatics* **11**, 7. https://doi.org/10.1186/1471-2105-11-7

Tang KSC, Konczak I, Zhao J (2017) Phenolic compounds of the Australian native herb *Prostanthera rotundifolia* and their biological activities. *Food Chemistry* **233**, 530–539. http://dx.doi.org/10.1016/j.foodchem.2017.04.137

Tate J, Simpson B (2003) Paraphyly of *Tarasa* (Malvaceae) and diverse origins of the polyploid species. *Systematic Botany* **28**, 723–737. https://doi.org/10.1043/02-64.1

Vos J, Joppa L, Gittleman J, Stephens P, Pimm S (2014) Estimating the normal background rate of species extinction. *Conservation Biology* **29**, 452–462. https://doi.org/10.1111/cobi.12380

Whitlock BA, Hale AM, Groff PA (2010) Intraspecific inversions pose a challenge for the *trn*H-*psb*A plant DNA barcode. *PLOS ONE* **5**, e11533. https://doi.org/10.1371/journal.pone.0011533

Wilson TC, Conn BJ, Henwood MJ (2012) Molecular phylogeny and systematics of *Prostanthera* (Lamiaceae). *Australian Systematic Botany* **25**, 341–352. https://doi.org/10.1071/SB12006

Wilson TC, Conn BJ, Henwood MJ (2017) Great expectations: Correlations between pollinator assemblages and floral characters in Lamiaceae. *International Journal of Plant Sciences* **178**, 170–187. https://doi.org/10.1086/690023

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Missing in the Shark Bay area, *Grevillea speckiana* Olde, a new species and the northernmost member of the *Triloba* Group (Proteaceae: Grevilleoideae: Hakeinae)

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Abstract

G. speckiana Olde is described from a single collection gathered in 1953. Although the specimens bears flowers in early bud, fruits and foliage are sufficient to assign and describe the species. Unlike several other species in the *Triloba* Group awaiting description from single specimens that represent extinct species, there is some hope for its continued existence because of the botanically unexplored locality in which it was collected.

Introduction

Grevillea speckiana is described from a single fruiting specimen at PERTH and one duplicate at CANB. The collection gathered in 1953 was first seen by me in 1999. Several trips were subsequently conducted by me and others in the Shark Bay region, to which a search for this species was admittedly incidental and confined to major roads, but based on a study of all N.H. Speck's collections made around the collecting date. Speck gathered his specimen from a locality geographically disjunct from where any other member of the *Triloba* group has been collected, previously restricted in its northernmost distribution in the south-west of Western Australia to the Murchison River. An anticipated confirming re-collection was hoped for, but regrettably has not yet come to pass.

Makinson (2000: 434) first treated the specimen as a doubtful record but included it in *G. biternata* Meisn., It has been recognised by the Western Australian herbarium in *FloraBase* as *Grevillea* sp. Shark Bay (N.H. Speck 24/09/1953) and was included by Gibson (2016: 156–7) among a group of species that are potentially extinct. A freely accessible image of the PERTH specimen given by Gibson and a helpful analysis of Speck's itinerary, give some hope that this species will be re-discovered in the largely remote and unexplored Shark Bay area. The epithet was selected after consultation with the updated list of fossil *Grevillea* epithets (Olde 2017).

Although simple leaves predominate on specimens of this and other species yet to be described in the *Triloba* Group, they rarely occur exclusively. A low percentage of bi- or divaricately tripartite leaves may also be present on any selected specimen and it is entirely possible that simple leaves will not always predominate a single collection. This paper is the fifth in a series aimed at revising the *Triloba* Group (Olde 2020; Olde 2021a, 2021b; Olde & Marriott 2021).

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Taxonomy

Grevillea speckiana Olde, *sp. nov.*

Type: Western Australia: Shark Bay [region], 24 Sep. 1953, *N.H. Speck s.n.* (holo: PERTH 01900609; iso: CANB 195204).

Morphologically similar to *Grevillea vestita* (Endl.) Meisn. but differing in its leaves mostly simple, linear, rarely once-divided with linear lobes. *Grevillea biternata* Meisn. differs in its rugose fruits.

Grevillea sp. Shark Bay (N.H. Speck 24/09/1953), Western Australian Herbarium, in *FloraBase*, https://florabase.dpaw.wa.gov.au [accessed 28 January 2016].

*Seedling*s not seen. *Mature plant* a *shrub* of unknown dimensions, shape and generative mode. *Branchlets* 0.8–2 mm thick, terete, not ribbed, grey-brown *in sicco*, pubescent-villous, the indumentum moderately dense, the hairs variable in length, spreading, straight or curved with white contents. *Adult leaves* usually simple, occasionally once-divided, bi-partite, very rarely divaricately tripartite; simple leaves 2–3 cm long, 1.2–1.3 mm wide, linear to narrowly elliptic, usually longitudinally incurved; divided leaves 2.5–3.2 cm long, 1.5–1.8 cm wide; leaves not crowded, ascending to patent, subsessile; *new growth* white-villous; *basal internode* (divided leaves) monomorphic, 13–15 mm long, 1.3–1.5 mm wide, narrowly cuneate, leaf base straight (simple leaves), elliptic in cross-section, villous, the adaxial surface flat to convex; *primary lobes* 2 or 3, 0.8–1 cm long, 1–1.3 mm wide, spreading, linear to narrowly elliptic, straight or recurved longitudinally, often slightly twisted, equal or slightly unequal, secondary division absent; *apices of leaves and lobes* acute, spinescent; *spine* 1.5–3 mm long, yellow-brown to dark brown, stiff, pungent; *margins* angularly refracted about the intramarginal vein, enclosing most but not all of the under-surface; *adaxial surface* flat to convex, moderately to densely tomentose-villous with a mixed indumentum of spreading hairs with arms of varying and sometimes unequal lengths filled with white contents, the midvein evident to impressed, straight, intramarginal and edge veins also evident, lateral veins not evident; *abaxial surface* bisulcate, the lamina enclosed, of divided leaves the lamina exposed below sinuses, sparsely villous, the midvein prominent, level with the revolute margin; *sulcae* 0.05–0.1 mm wide, villous; *texture* coriaceous; *petioles* 0.1–0.7 mm long, 1–1.2 mm wide, normal, obscure, 3-merous, spreading slightly at the point of attachment, the central segment not developed down the branch, the lateral segments spreading, the adaxial surface concave, glabrous or sometimes with scattered hairs; the abaxial surface convex, sparsely villous. *Conflorescences* axillary, occasionally subterminal on short axillary branches, simple or rarely, 2-branched at the base, enclosed within the foliage, extending well down the branch; *unit conflorescences* c. 1 cm diam., shape indeterminate ?globose, moderately dense, petaly uncertain, probably acropetal; *buds* 2 mm long, 1.8 mm wide, ovoid, sessile to very shortly pedunculate, enclosed by bracts or bractiform leaves, swelling and proceeding to immediate development; *peduncles* 0–2 mm long, villous; *floral rachises* 5–11 mm long, tapering distally, white-tomentose to-villous, hairs sparse at the base, twisted, not extending beyond the outline of prominent floral nodes, the nodes condensed towards apex; *involucral bracts* 2–2.5 mm long, 0.8 mm wide, ovate-acuminate, tomentose, the hairs moderately dense, more so at the apex than the base; *common bracts* 0.7–1.5 mm long, 0.5–1 mm wide, ovate, sharply to smoothly recurved from *c.* halfway, flat (not cymbiform), sparsely villous abaxially, persistent to fruiting. *Flower colour green* in bud. *Flowers* actinomorphic, glabrous externally, not discolorous *in sicco*; *pedicels* 7–12 mm long, ascending, the apex abruptly expanded, an aberrant pedicel conjoined above its base with a fruit-bearing pedicel; *torus* 0.6–0.7 mm across, slightly oblique; *nectary* evident, U-shaped, rising 0.1 mm above the torus, margin entire; *pistil* not seen (see fructual style below); *perianth* 4.2 mm long, the tube 3 mm long, 0.7 mm wide, subcylindrical to narrowly obovoid; *limb* 1.2 mm long, 1.5 mm wide, spheroidal; *tepal-limbs* 0.75 mm wide, keeled; *pollen*: yellow, triporate; abnormalities not observed. *Fruits* follicular, 7.5–9.5 mm long, 4.5 mm wide, transverse on incurved pedicel, with attachment subposterior 2–3 mm from base, oblong-ellipsoidal; fructual style lateral with pollen-presenter conical, straight-sided, 0.6 mm long, 0.35 mm wide at base, the base slightly to markedly oblique, abruptly divergent from the style-end, scarcely to very narrowly rimmed; stylar dilation ovoid, 0.8–1 mm wide contracting to 0.5 mm immediately below the pollen-presenter; stigma 0.1 mm wide, not oblique; pericarp *c.* 0.4 mm thick; exocarp smooth to slightly colliculose; *mesocarp* crustaceous; *endocarp* smooth, membranaceous. *Seeds* (immature) (CANB 195204 in pkt) 3 mm long, 1 mm wide at apex, 0.6 mm wide at base, biconvex, obovoid, winged at apex with an excurrent apical wing 0.5 mm long, smooth on the outer face, flanged on the inner face with an obscure submarginal, waxy collar. (Figures 1, 2)

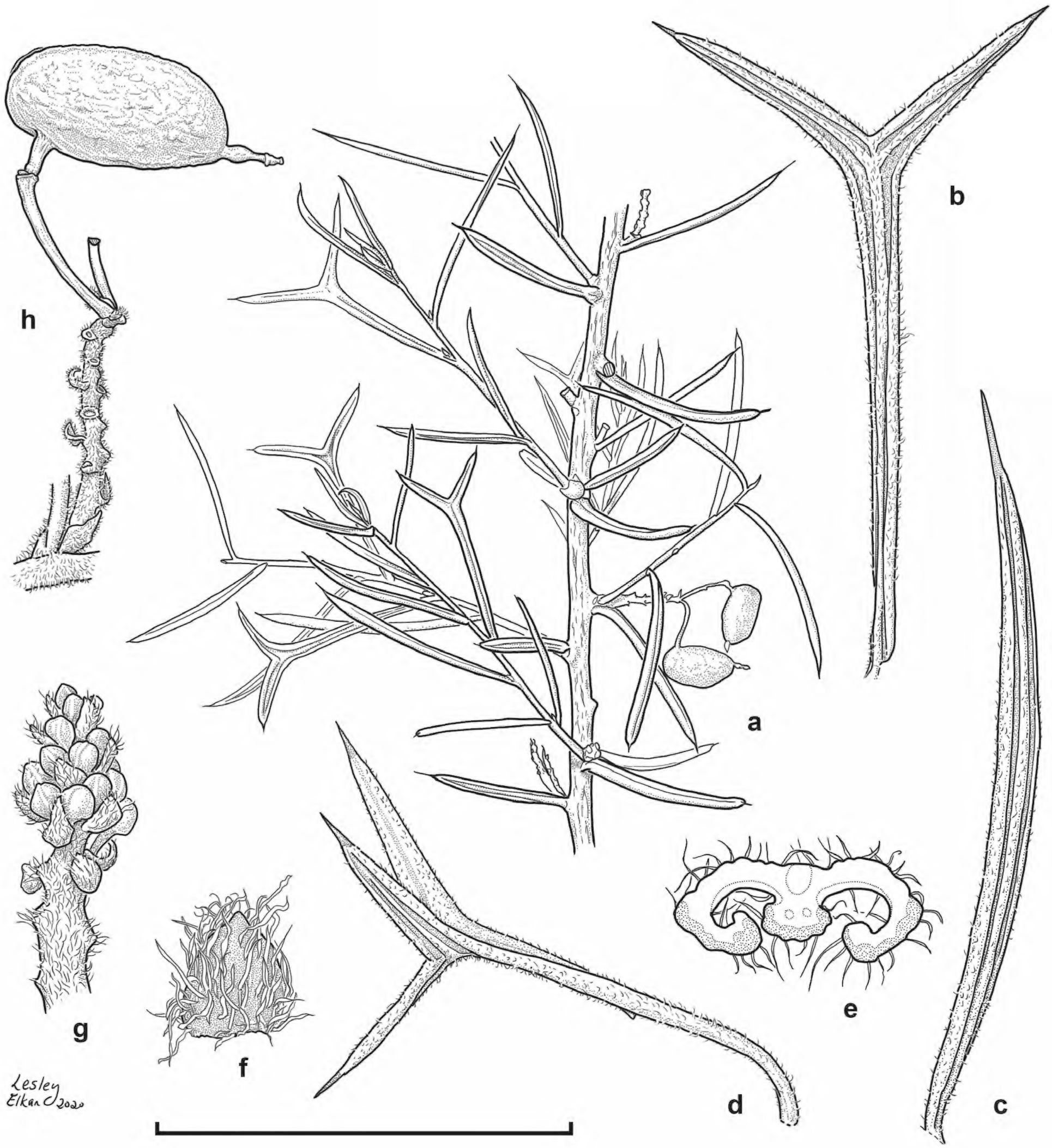

Fig. 1. *Grevillea speckiana*. a. Fruiting branch. b. Leaf with divided apex. c. Leaf with simple blade. d. Leaf with trifurcate apex (lateral view). e. Transverse section of leaf. f. Bract. g. conflorescence in bud. h. Persistent follicle. Scale bar: a = 50 mm; b–d, h = 15 mm; e = 2 mm; f = 2.5 mm; g = 7.5 mm. Illustration by Lesley Elkan from *H.N. Speck s.n.*, 24/09/1953 (holotype; PERTH 01900609).

Diagnostic characters: Branchlets pubescent-villous, the indumentum moderately dense. Leaves mostly simple, a few once-divided bi- to divaricately tripartite; simple leaves ≤1.3 mm wide, linear to very narrowly elliptic, usually longitudinally curved, divided leaves occasional, forked; floral rachises 5–11 mm long, white-tomentose-villous; common bracts sparsely villous on the outer surface, persistent; pedicels 7–12 mm long; nectary prominent; fructual style glabrous, dilated up to 1 mm wide; pollen-presenter conical; perianth outer surface glabrous, actinomorphic; fruits with smooth exocarp.

Distribution: Western Australia where known only from the Shark Bay area. It occurs apparently in the Shark Bay LGA, in the Wooramel Subregion of the Carnarvon IBRA Region. Gibson (2016: 156) suggests a locality between Hamelin Pool and Carnarvon as most likely.

Fig. 2. Isotype of *Grevillea speckiana* (CANB 195204). Photo by P. Olde.

Doubt has been expressed about the accuracy of Speck's location and suggestions have been made that the collection is more likely to have been made near the old coastal highway, although this is speculative. Extensive collections in the tree heath and a flora survey of Hamelin Station for Bush Heritage failed to record this species. Two possibilities can be entertained.

1. If *G. speckiana* is a rare seed-obligate species, then as with some other declared rare flora, an intense fire in the region may stimulate growth from the stored seed bank.
2. The species may have been collected on the Victoria Plateau, not the Peron region of Shark Bay, where the red sands of the tree heath occurs. This area contains the Eurady and Nerren Nerren Dune Systems that contain many unusual and local endemics. He was in and around this area (Junga Tank and 46 mile tank) on 22 and 25 of September 1953 and also collected *Banksia lindleyana* labelled as south of Hamelin and *Banksia ashbyi* previously (on 9-1945) also labelled as south of Hamelin Pool. None of these collections are site specific but relate to the area around a feature. All can be located on the main highway. The WA Wildflower Society surveyed Eurady Station for Bush Heritage and did not locate any *Grevillea* matching this species. However, there are large areas of sandplain country to the north located on Unallocated Crown Land, Nerren-Nerren and Coburn Stations, all of which reach the main highway, and which are relatively unexplored.

Phenology: Flowering probably commences in autumn and is finished by late winter; fruits apparently form abundantly in early spring, but may be subject to periodic rainfall.

Habitat and ecology: Unknown. It probably occurs in Eremaean Proteaceae woodland. There is a flower of an unidentified proteaceous plant (possibly *Banksia*) entangled in the foliage of the PERTH specimen which, when identified, may give a clue to the plant association of this species. Speck did not collect a *Banksia* on this day and the flower may form a natural co-occurrence with *Grevillea speckiana*.

Specimens seen: Only known from the type collection.

Conservation status: A conservation code for Western Australian Flora of Priority One has been assigned to this species by the Western Australian Herbarium (1998–).

Etymology: The specific epithet honours Nathaniel Henry Speck (1906–1970), science teacher and later plant ecologist and plant biogeographer whose field work and plant collections resulted in the discovery of many new species.

Discussion: *Grevillea speckiana* appears to share some significant morphological features with *G. vestita* including foliar indumentum, persistent common bracts, a conical pollen-presenter, and smooth to very faintly colliculose follicles bearing similar attached styles.

It differs in its mostly simple, linear leaves of which there are none in known populations of *G. vestita*. Morphological similarities do not imply that taxa should be treated as the same species or even subordinated as subspecies, at least until some scientific proof and phylogenetic analysis is put forward as evidence.

A separate undescribed species, probably related to *G. levis* Olde & Marriott, has been collected in the Kalbarri–Murchison River area. It has divaricately tripartite to biternate leaves, occasional simple leaves, smooth fruits and hairy branchlets. This species is currently under study, interrupted by access to specimens, and will be the subject of a future paper. It differs from *G. speckiana* in its appressed foliar indumentum, its leaves and lobes narrower and some with secondary division, its common bracts early caducous. The undescribed taxon differs from *G. levis* in its hairy branchlets, though a full suite of differentiating characters awaits the study of the morphologically diverse *G. levis* across its entire distribution. *G. biternata* differs in its rugose fruits and is also the subject of ongoing revision. *G. triloba* occurs between Northampton and Geraldton. It has rugose fruits and its leaves also have prominent secondary venation on the leaf upper surface, especially noticeable in dried specimens. In some forms simple leaves predominate, a likely source of some confusion if fruits are lacking.

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References

Gibson N (2016) Western Australian plant taxa not collected for more than 50 years. *Nuytsia* 27: 139–164. https://florabase.dpaw.wa.gov.au/science/nuytsia/787.pdf

Gibson N, Keighery GJ, Keighery BJ (1997) Contributions of N H Speck to the biogeography of Proteaceae in Western Australia. *Journal of the Royal Society of Western Australia* 80: 73–77. https://www.rswa.org.au/publications/Journal/80(2)/80(2)gibson.pdf

McGillivray DJ & Makinson RO (1993) Grevillea, *Proteaceae: a taxonomic revision.* (Melbourne University Press: Carlton, Victoria)

Makinson RO (2000) Proteaceae 2, *Grevillea*. *Flora of Australia*. Volume 17A. (Australian Biological Resources Study: Canberra)

Olde PM (2017) A preliminary checklist of fossil names in extant genera of the Proteaceae. *Telopea* 20: 289–324. https://dx.doi.org/10.7751/telopea10644

Olde PM (2020) *Grevillea pieroniae* Olde (Proteaceae: Grevilleoideae: Hakeinae), a rare new species in the *Triloba* Group from the Stirling Range, Western Australia, and a short history of the group. *Telopea* 23: 227–235. http://dx.doi.org/10.7751/telopea14783

Olde PM (2021a) *Grevillea hortiorum* Olde (Proteaceae: Grevilleoideae: Hakeinae), an uncommon species from winter-damp woodlands in the Avon Wheatbelt, south-west Western Australia. *Telopea* 24: 1–6. http://dx.doi.org/10.7751/telopea14823

Olde PM (2021b) *Grevillea trichantha*, a third species with hairy flowers in the *Triloba* Group (Proteaceae: Grevilleoideae: Hakeinae) from the Marchagee Track, south-west Western Australia. *Telopea* 24: In press. http://dx.doi.org/10.7751/telopea15325

Olde PM, Marriott NR (1994) *The* Grevillea *Book Vol. 1*. (Kangaroo Press: Kenthurst, New South Wales)

Olde PM, Marriott NR (1995a) *The* Grevillea *Book Vol. 2*. (Kangaroo Press: Kenthurst, New South Wales)

Olde PM, Marriott NR (1995b) *The* Grevillea *Book Vol. 3*. (Kangaroo Press: Kenthurst, New South Wales)

Olde PM, Marriott NR (2021) *Grevillea merceri* Olde & Marriott (Proteaceae: Grevilleoideae: Hakeinae) an uncommon, geographically isolated species in the *Triloba* Group from subcoastal areas of southern Western Australia. *Telopea* 24: 241–245. http://dx.doi.org/10.7751/telopea14797

Western Australian Herbarium (1988–) Florabase. *Grevillea* sp. Shark Bay (N.H. Speck 24/09/1953). https://florabase.dpaw.wa.gov.au/browse/profile/19192

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New Philippine moss records and additions to the Luzon moss flora

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Abstract

Four new Philippine moss records and five additions for the Luzon moss flora are presented. *Anomodontopsis rugelii* (Müll. Hal.) Ignatov & Fedosov; *Chaetomitrium horridulum* Bosch & Sande Lac.; *Chaetomitrium vrieseanum* Bosch & Sande Lac.; and *Dicranoloma deplanchei* (Duby) Par. are new country moss records while *Anomodon pseudotristis* (Müll. Hal.) Kindb.; *Bescherellia elegantissima* Duby; *Claopodium assurgens* (Sull. & Lesq.) Cardot; *Pseudoparaphysanthus moutieri* (Broth. & Paris) S.Olsson, Enroth, Huttunen & D.Quandt and *Racopilum magnirete* E.B.Bartram are new additions to the Luzon moss flora. *Anomodontopsis* Ignatov & Fedosov is a new genus record for the Philippines. This report of new records for the Philippine and Luzon's moss flora has once again highlighted the importance of continued bryological studies in the archipelago. In this respect, field collecting in the country's intervening islands and understudied areas is still necessary to further improve of knowledge of Philippine moss flora.

Introduction

The author's review of bryophyte collections kept at the Philippine National Herbarium (code, PNH) and his expeditions to under-studied areas of the country have yielded four species of mosses new to the country and five new records for the Luzon moss flora. Among these new Philippine records, *Anomodontopsis rugelii* (Müll. Hal.) Ignatov & Fedosov; *Chaetomitrium vrieseanum* Bosch & Sande Lac.; and *Dicranoloma deplanchei* (Duby) Par. are also new records for Luzon while *Chaetomitrium horridulum* Bosch & Sande Lac. is reported here for the first time for Mindoro island. *Chaetomitrium horridulum*, *C. vrieseanum* and *D. deplanchei* are rather restricted in distribution, at least in Southeast Asia while *A. rugelii* is rather widespread in the temperate northern hemisphere. *Anomodontopsis* Ignatov & Fedosov is a new genus record for the Philippines.

In the case of the mosses added to the Luzon's moss flora, these are rather significant. *Bescherellia elegantissima* Duby, *Claopodium assurgens* (Sull. & Lesq.) Cardot and *Racopilum magnirete* E.B.Bartram are previously known in the Philippines only in Mindanao island. *Anomodon pseudotristis* (Müll. Hal.) Kindb., on the other hand, has only been recorded in Leyte and Mindoro islands while *Pseudoparaphysanthus moutieri* (Broth. & Paris) S.Olsson, Enroth, Huttunen & D.Quandt has been reported from a single locality in Samar island. Interestingly, the new Luzon materials of *A. pseudotristis*, *B. elegantissima*, *C. assurgens* and *R. magnirete* are author's collections from Mingan Mountains in the Sierra Madre Mountain Range while the single *P. moutieri* collection that has been kept in the PNH came from Mount Isarog. Both localities now represent

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the northernmost stations in the archipelago for *A. pseudotristis*, *B. elegantissima* and *R. magnirete*, except *C. assurgens* which was earlier reported by Tan and Iwatsuki (1983) in the small island of Batan found in the far northern end of the country. Likewise, these Mingan Mountains and Mount Isarog records also foretell the likely presence of these species in other parts of Luzon.

Identification of the abovementioned mosses followed Akiyama and Suleiman 2001; Bartram 1944; Enroth 1990; Fife 2014; Fleischer 1906-1908; Granzow-de la Cerda 1997; Noguchi *et al.* 1991; Pursell and Reese 1982; Sastre-De Jesús 1987; Suleiman and Anwar 2021; Tan 1987; Tan and Iwatsuki 1983; Touw 1972; Touw and Ochyra 1987; and van Zanten 2006. Their status, on the other hand, has been verified from floristic studies (Akiyama and Suleiman 2001; Ariyanti *et al.* 2009; Azuelo *et al.* 2015; Fife 2014; Fleischer 1915-1922; Granzow-de la Cerda 1997; Klazenga 1999; Linis 2004, 2006, 2009, 2010, 2014, 2018, 2019a, b; Linis and Tan 2008, 2010, 2013; Lubos 2010; Noguchi *et al.* 1991; Pócs 1969; Shevock and Yorong 2018; Suleiman and Akiyama 2014; Tan 1987; Tan and Iwatsuki 1983, 91; Tan and Robinson 1990; Tan and Shevock 2014, 2015; and Tan *et al.* 2000, 2015; Thin 1997; Thouvenot and Bardat 2013; Wu *et al.* 2002, 2011; van Zanten 2006). In addition, several type and Asian specimens lodged in BM, CAHP, PNH and SIN are examined to confirm their identities. Classification system of the identified species presented is adopted from Goffinet *et al.* (2009) while species authority name abbreviations are based on Brummitt and Powell (1992). Vouchered moss specimens are lodged in the PNH. The new Philippine and Luzon moss records are listed in alphabetical order.

New Philippine moss records

Anomodontopsis rugelii (Müll. Hal.) Ignatov & Fedosov., *Arctoa* 28(1): 90. 2019. (Anomodontaceae)

The recent molecular phylogenetic analysis of the genus *Anomodon* proposed the segregation of *Anomodon rugelii* (Müll. Hal.) Keissl. after finding it to be distant from the core *Anomodon* clade (Ignatov *et al.* 2019). This led to the transferring of *A. rugelii* into a new genus *Anomodontopsis* Ignatov & Fedosov within the Anomodontaceae. Despite lacking an obvious morphological synapomorphy, however, the author has accepted this proposal and named the Philippine specimen of *Anomodon rugelii* as *Anomodontopsis rugelii* (Müll. Hal.) Ignatov & Fedosov.

Distinctively slender in rusty brownish dense mats, the Philippine *A. rugelii* plant (Fig. 1) is essentially distinguishable in the field by its dry, incurving leaves, reddish costa and the conspicuous auricles found at the bases of its leaves (Granzow-de la Cerda 1997). Under the microscope, the leaf costa in *A. rugelii* are smooth abaxially with highly raised papillose-mamillose cells on the basal leaf margins and on the auricles. The presence of foliose uniseriate pseudoparaphyllia, which are absent in *Anomodon* species, is also helpful in distinguishing *A. rugelii*.

Extra-Philippine Distribution: Mainly circumboreal in Asia, eastern North America, and Central Europe (Granzow-de la Cerda 1997). **Intra-Philippine Distribution:** New to the Philippines. **Specimen examined:** Imelda Park, Baguio City, Benguet Province, Luzon Island, Philippines, on branches, 11 July 1987, *R. Magill, P. Redfearn and M. Crosby 8087* as *Anomodon rugelii* (Müll. Hal.) Keissl. det. *P. Redfearn* (PNH180043).

Chaetomitrium horridulum Bosch & Sande Lac. *Bryologia Javanica* 2: 46. 167. 1862. (Symphyodontaceae)

Chaetomitrium horridulum is a Malesian endemic reported here for the Philippines for the first time. The Philippine material identified as *C. horridulum* (Fig. 2) has setulose seta up to 3 cm long and has a plant size distinctly larger compared to other Philippine *Chaetomitrium* species. Other morphological characters of this material agree well with the original description provided by Fleischer (1906–1908), hence, can be recognised by its reddish-brown colouration, widely spreading lanceolate leaves, smooth lamina cells and cucullate calyptra which are hispid above and without cilia at the base.

Elsewhere, *C. horridulum* can only be confused with *C. ciliatum*, another Malesian endemic. Both species are similar in appearance but the latter has no reddish-coloration tinge and has much denser, spinose-prorate lamina cells on the abaxial surfaces of its leaves. According to Suleiman and Akiyama (2014), *C. ciliatum* could be a variant of *C. horridulum*.

Extra-Philippine Distribution: Borneo, Java, and Sumatra (Akiyama and Suleiman 2001; Suleiman and Akiyama 2014). **Intra-Philippine Distribution:** New to the Philippines. **Specimen examined:** Mount Ayniaban, Puerto Galera, Province of Mindoro Oriental, Mindoro Island, Philippines, on bark of trees, 5 March 1989, *J. R. Cabalguinto and B. O. van Zanten 997* (PNH).

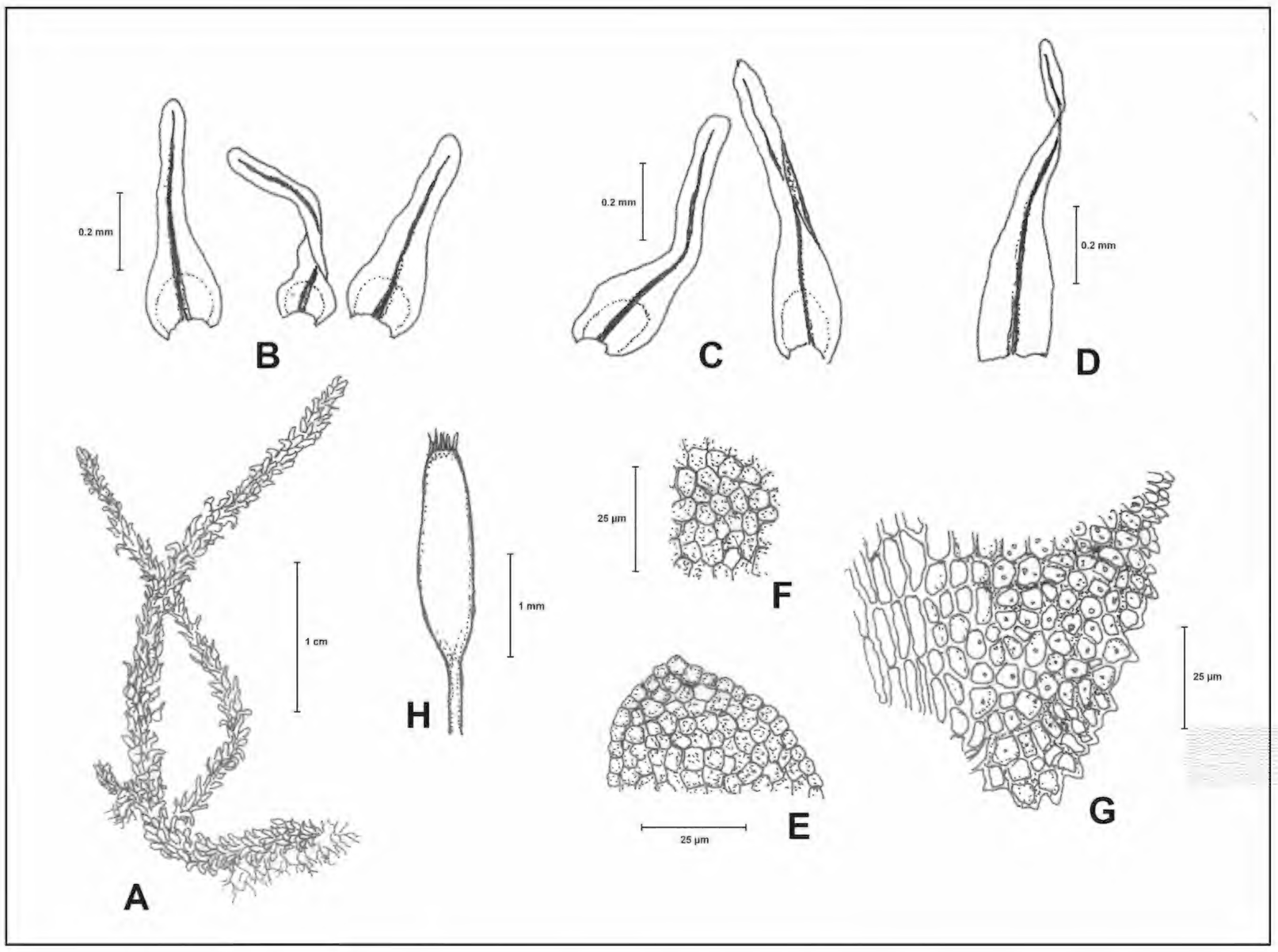

Fig. 1. *Anomodontopsis rugelii* (Müll. Hal.) Ignatov & Fedosov. (A) Habit. (B) Branch leaves. (C) Stem leaves. (D) Perichaetial leaf. (E) Apex of branch leaf. (F) Median laminal cells adjacent to margin of branch leaf. (G) Basal laminal cells near costa of leaf. (H) Capsule. (All from *R. Magill, P. Redfearn and M. Crosby 8087* (PNH)).

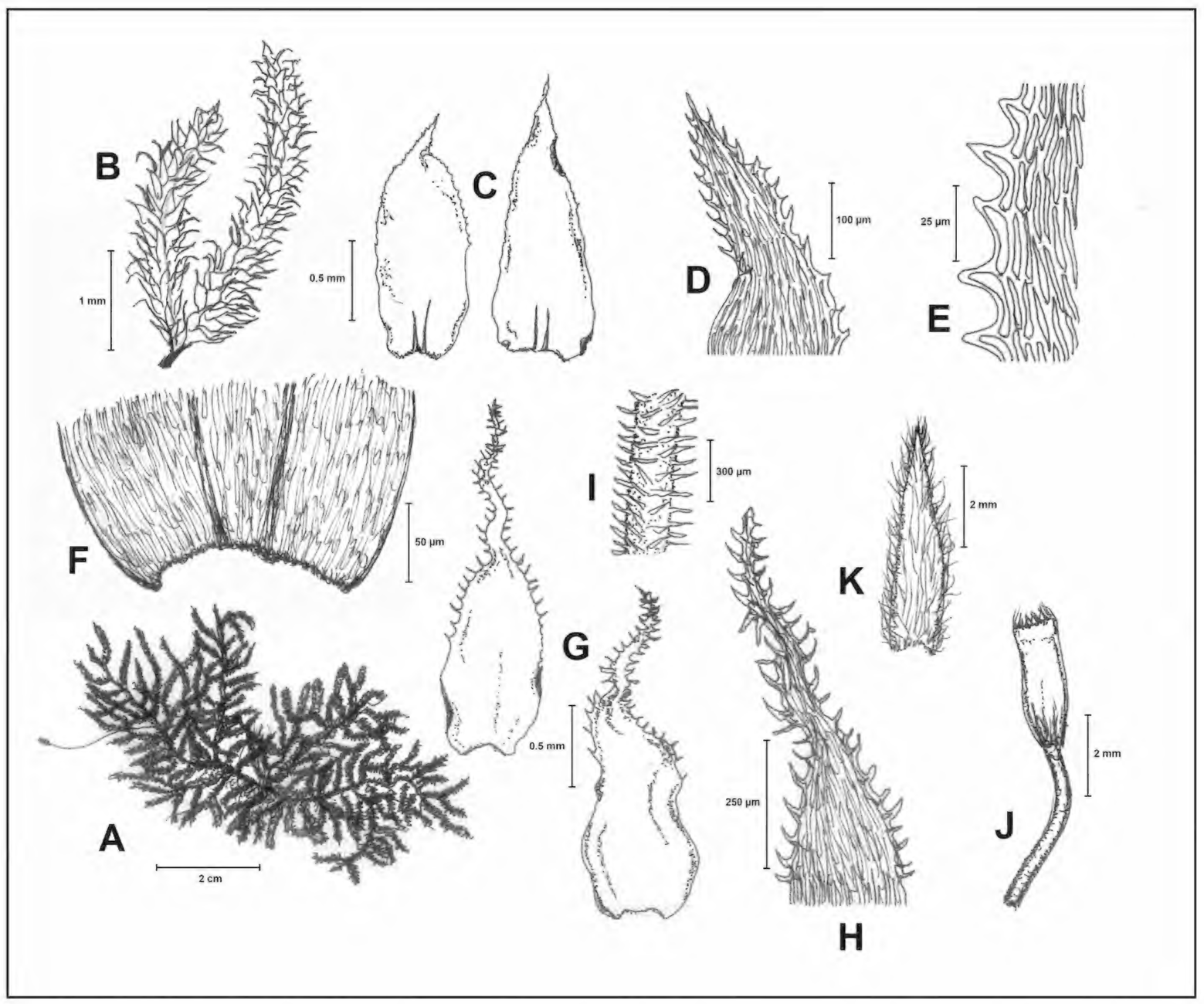

Fig. 2. *Chaetomitrium horridulum* Bosch & Sande Lac. (A) Habit. (B) Portion of shoot. (C) Branch leaves. (D) Apex of branch leaf. (E) Median laminal cells of branch leaf. (F) Basal laminal cells of branch leaf. (G) Inner perichaetial leaves. (H) Apex of perichaetial leaf. (I) Ornamentation on a seta. (J) Capsule. (K) Calyptra. (All from *J. R. Cabalguinto and B. O. van Zanten 997* (PNH)).

Chaetomitrium vrieseanum Bosch & Sande Lac., *Bryologia Javanica* 2: 54. 174. 1862. (Symphyodontaceae)

Chaetomitrium vrieseanum is one of the smaller members of the genus. Together with *C. acanthocarpum* Bosch & Sande Lac., *C. brassii* E.B.Bartram, *C. laevisetum* Dixon, *C. robbinsii* E.B.Bartram, and *C. roemeri* M.Fleisch., it belongs to a subgroup under *Chaetomitrium* that has orbicular to suborbicular branch leaves (Suleiman and Anwar 2021). Until recently, this subgroup has been known to be restricted in New Guinea and neighbouring islands. However, the reporting of *C. acanthocarpum* in Sulawesi by Ariyanti *et al.* (2009) and the recent discovery of *C. vrieseanum* in Borneo by Suleiman and Anwar (2021) have extended the geographical distribution of this subgroup to the West Malesian region.

Chaetomitrium vrieseanum (Fig. 3) is unlike other Philippine species of *Chaetomitrium*. Apart from its small size, it can be easily distinguished from other local congeners by its squarrose, orbicular branch leaves with margins that are strongly undulate above which end in rounded apices with sharp apiculus (Suleiman and Anwar 2021). The only other Philippine member of *Chaetomitrium* that comes close to it in terms of size is *C. leptopoma* (Schwägr.) Bosch & Sande Lac. However, the branch leaves of the latter, although shortly apiculate, are rather ovate and rigid which are erect or recurved at apices (Suleiman and Akiyama 2014).

Extra-Philippine Distribution: Borneo (Suleiman and Anwar 2021), New Guinea (Akiyama 1997) and Seram Island of the Maluku Islands, Indonesia (Akiyama and Suleiman 2014). **Intra-Philippine Distribution:** New to the Philippines. **Specimen examined:** North slope of Mount Isarog, Province of Camarines Sur, Luzon Island, Philippines, on branches, 18 May 1991, *J. R. Cabalguinto 2182* (PNH).

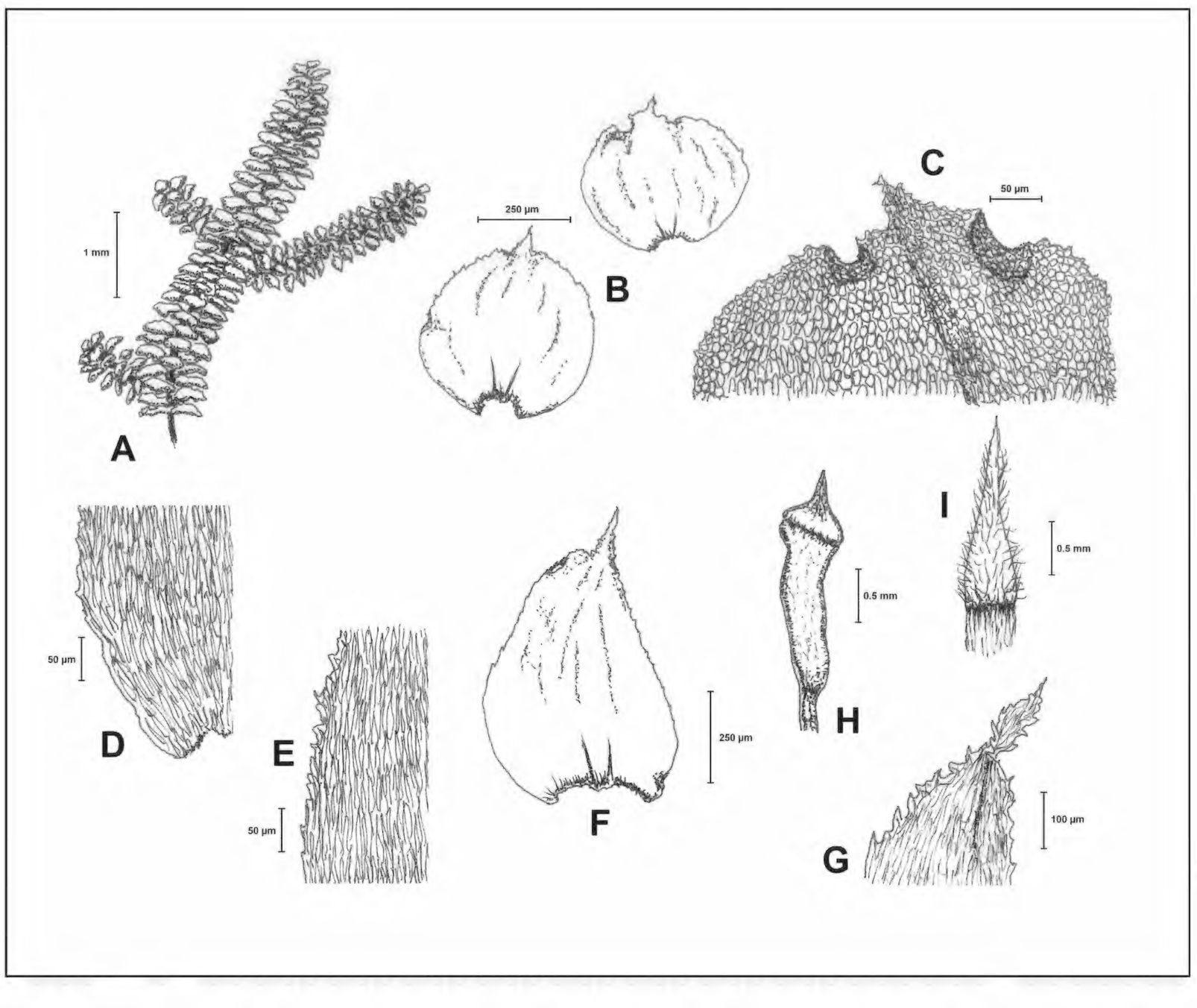

Fig. 3. *Chaetomitrium vrieseanum* Bosch & Sande Lac. (A) Portion of shoot. (B) Branch leaves. (C) Apex of branch leaf. (D) Basal laminal cells of branch leaf. (E) Median laminal cells of branch leaf. (F) Inner perichaetial leaf. (G) Apex of inner perichaetial leaf. (H) Capsule. (I) Calyptra. (All from *J. R. Cabalguinto* 2182 (PNH)).

Dicranoloma deplanchei (Duby) Par., *Index Bryologicus, editio secunda* 2: 25. 1904. (Dicranaceae)

Having been found on soil, the Philippine *Dicranoloma deplanchei* material (Fig. 4) resembles a diminutive form of *D. billarderii* (Brid.) Paris with elongate to linear, thick-walled upper lamina cells, serrated leaf margins, and a costa with scattered abaxial teeth. However, the morphological characters of this *D. deplanchei* material conform to that of Pursell and Reese (1982)'s description of the species with weaker serrulations along leaf margins, thinner-walled lamina cells, and fewer teeth on the abaxial surfaces of the costa. In *D. billarderii*, the leaves are generally secund, distinctly ventrally secund along with the shoots (Fife 2019), unlike

D. deplanchei leaves (Fig. 4A). The leaf shape in *D. deplanchei* is much different from *D. billarderii*, which is broader at the base than the more linear leaf shape of *D. deplanchei* (Fig. 4B). Also, the walls of alar cells in the *D. deplanchei* leaves are darker orange to brown in colour, somewhat thicker, and never with angular thickenings. Furthermore, the leaf costae in *D. deplanchei* are found to consist of more than three guide cells with at least two tiers of stereid bands above and below these cells (Fig. 4D) as in the case of leaf costae in *D. billarderii,* which consist of 2, rarely up to 3 guide cells which have only one tier of stereid band above and below these cells (Fife 2019).

In the meantime, the author will use the abovementioned morphological distinctions to keep *D. deplanchei* and *D. billarderii* apart. This treatment will remain until sufficient evidence become available to prove the two species inseparable.

Extra-Philippine Distribution: New Caledonia and New Guinea (Pursell and Reese 1982). **Intra-Philippine Distribution:** New to the Philippines. **Specimen examined:** Ating Tahanan, Baguio City, Benguet Province, Luzon Island, Philippines, on soil, May 13, 1991, *P. P. Lowry II and B. Suprin 3703* (PNH180033).

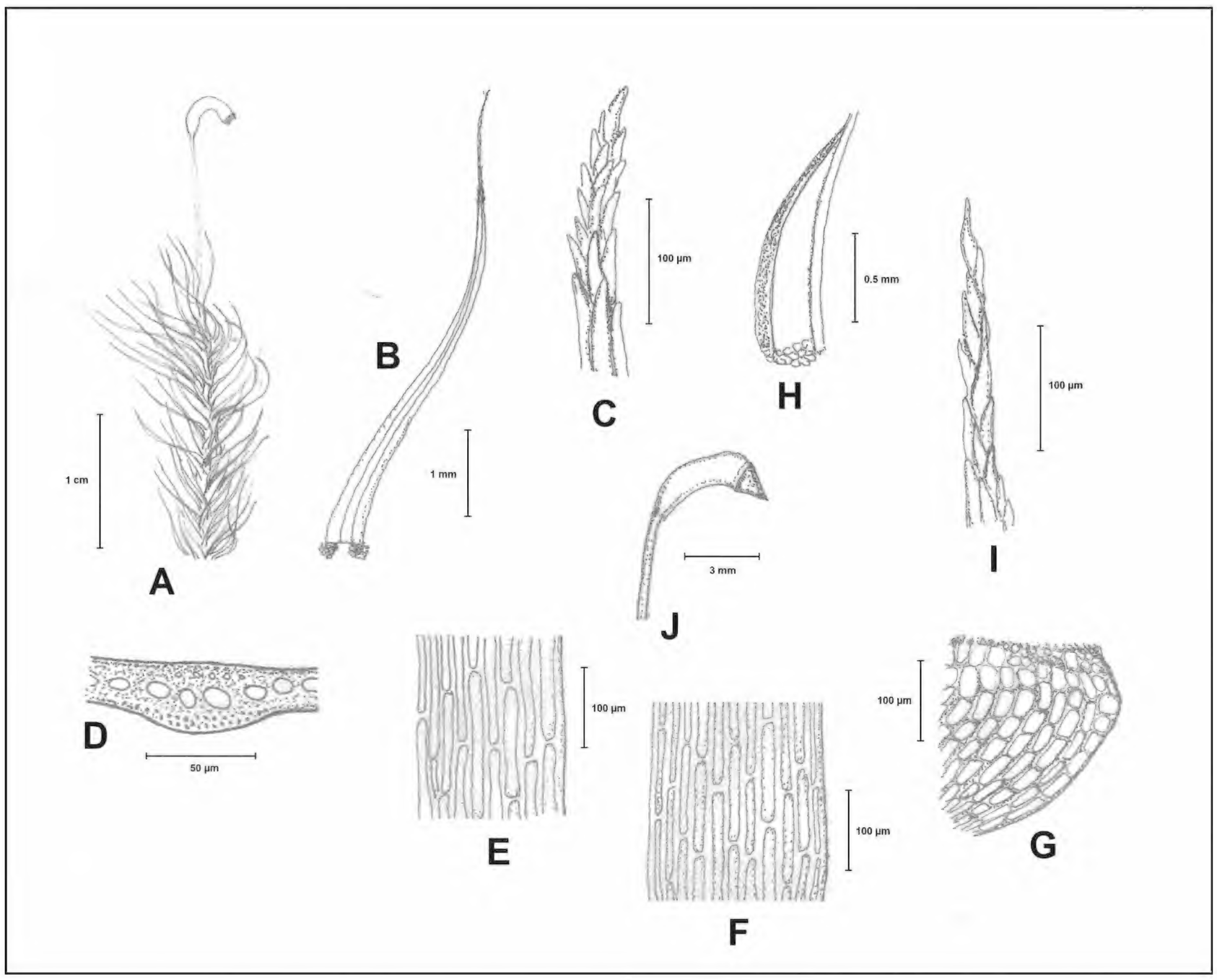

Fig. 4. *Dicranoloma deplanchei* (Duby) Par. (A) Portion of shoot. (B) Leaf. (C) Apex of leaf. (D) Cross-section of leaf through the costa just above the alar patches. (E) Median laminal cells of leaf. (F) Basal laminal cells of leaf. (G) Alar cells. (H) Lower part of an inner perichaetial leaf. (I) Apex of inner perichaetial leaf. (J) Capsule. (All from *P. P. Lowry II and B. Suprin 3703* (PNH180033)).

Additions to Luzon moss flora

Anomodon pseudotristis (Müll. Hal.) Kindb., *Enumeratio Bryinearum Exoticarum, Supplementum Secundum* 97. 1891. (Anomodontaceae)

The Mingan plant identified as *A. pseudotristis* (Fig. 5) is very similar to other Asian *A. pseudotristis* plant materials examined by the author (Mount Ma-Tou, Jiangsu Province, China, *M. C. Ji 12700* (SIN); Tosashimizu-shi, Shikoku, Japan, *H. Deguchi s.n.* (SIN); Mount Pangasugan, Baybay City, Leyte Province, Leyte Island, Philippines, *B.C. Tan, M. Navarez and L. Raros 84-230* (CAHP); Mount Baco, Mindoro Occidental Province, Mindoro Island, Philippines, *V. C. Linis 1289-05* (PNH)) except the Mingan plant is much smaller, barely exceeding 1.4 cm in length.

In the Philippines, *A. pseudotristis* is readily distinguishable from its local congener *A. viticulosus* (Hedw.) Hook. & Taylor (Linis and Tan 2010). However, *A. viticulosus* is a larger plant (ca. 6–9 cm long) in dense mats with lingulate branch leaves (up to 3 mm long) that gradually taper to narrow lingulate smooth apices whereas *A. pseudotristis* is a much smaller plant in thin mats with tiny lingulate branch leaves (under 0.5 mm long) that end in rounded, obtuse to broadly acute leaf apices which are crenulate throughout due to prominent papillae. Furthermore, *A. viticulosus* is generally observed growing on calcareous soils (Noguchi *et al.* 1991; Linis and Tan 2010) whereas *A. pseudotristis* is entirely epiphytic on dicotyledonous trees (Tan 1987; Noguchi *et al.* 1991; Linis 2009; Fife 2014).

Extra-Philippine Distribution: Widely distributed in regions around Indian Ocean and Southwest Pacific and is one of the few in the genus to reach the Southern Hemisphere (Noguchi *et al.* 1991; Granzow-de la Cerda 1997; Thouvenot and Bardat 2013; Fife 2014). **Intra-Philippine Distribution:** Leyte (Tan 1987; Tan and Iwatsuki 1991) and Mindoro islands (Linis 2009). **Specimen examined:** So. Siete, Mingan Mountains, Gabaldon, Nueva Ecija Province, Luzon Island, Philippines, on trunk of Aymit (*Ficus* sp.) tree, November 3, 2007, 460 m a.s.l., 15° 29.00' 21.58" N 121° 20.00' 48.79" E, *V. C. Linis 2737-07* (PNH).

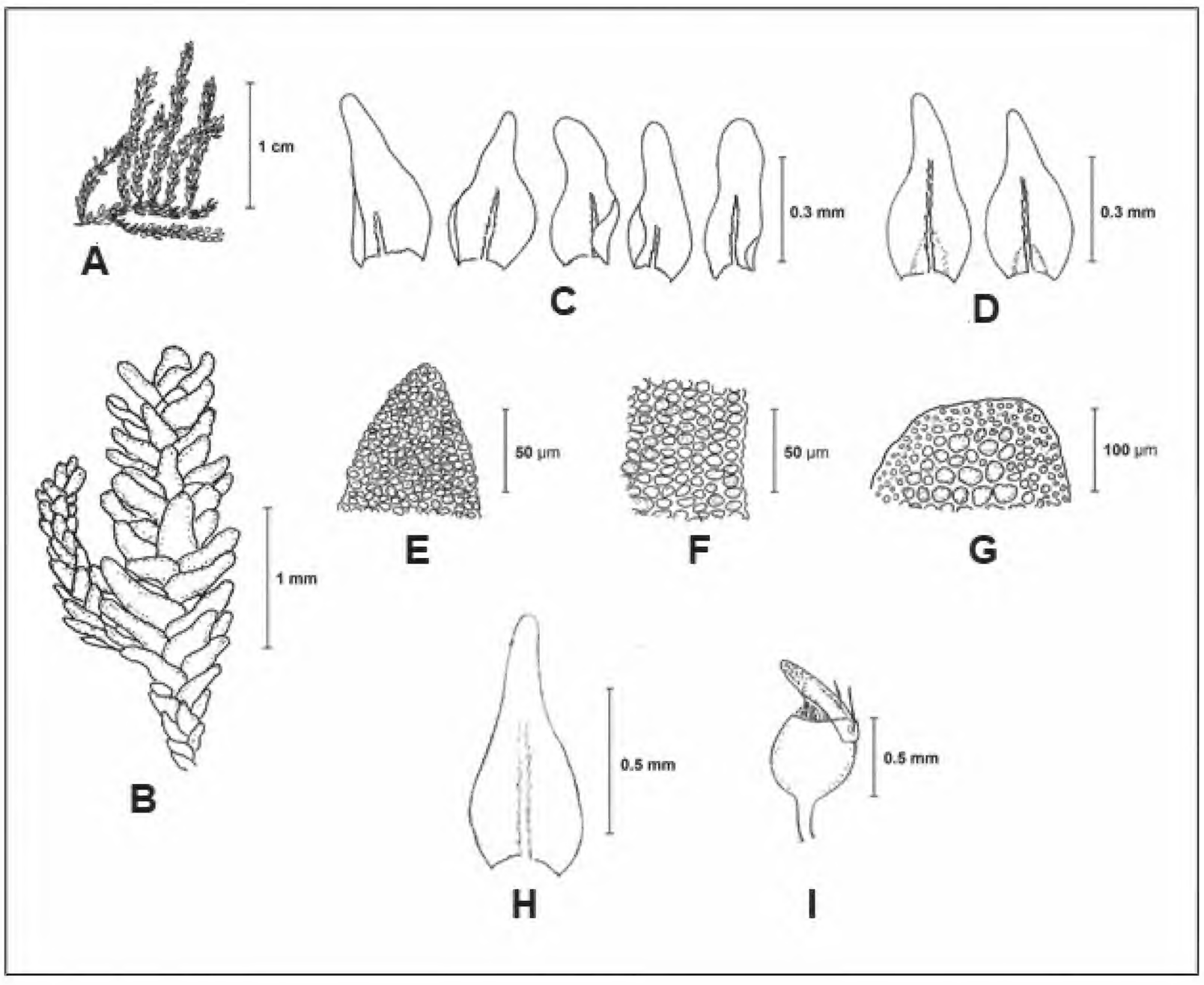

Fig. 5. *Anomodon pseudotristis* (Müll. Hal.) Kindb. (A) Habit. (B) Portion of shoot. (C) Branch leaves. (D) Stem leaves. (E) Apex of branch leaf. (F) Median laminal cells adjacent to margin of branch leaf. (G) Cross section of stem. (H) Inner perichaetial leaf. (I) Capsule. (All from *Linis 2737-07* (PNH)).

Bescherellia elegantissima Duby, *Bulletin de la Société Botanique de France* 20: 130. 1. 1873. (Hypnodendraceae)

Examination of the type material of *B. philippinensis* (Zamboanga, Mindanao Philippines, *E. D. Merrill 8354* (BM000986837)) and the Mingan plant materials has shown that both are morphologically similar except the leaves in Mingan plants are slightly longer (ca. 3.0–7.0 mm long) with more abruptly narrowed lamina, longer subula and serrated margins (Fig. 6). Therefore, the author is maintaining them as one species until definitive evidence is available to prove otherwise.

The discovery of *B. elegantissima* in Mingan Mountains more than 80 years after its first collection by Merrill from Zamboanga province in Mindanao island (Bartram, 1939) reveals a significant extension of its extant Philippine range from the western Mindanao bordering the South China Sea to the eastern coast of Luzon island alongside the Pacific Ocean.

Extra-Philippine Distribution: Australia, New Guinea, New Zealand, and Sulawesi (Sastre-De Jesús 1987; Enroth 1990). **Intra-Philippine Distribution:** Mindanao (Bartram 1939; Tan and Iwatsuki 1991). **Specimens examined:** Mt. Hugis Balanga, Mingan Mountains, Aurora Province, Luzon Island, Philippines, on tree trunk, lowland forest., November 4, 2007, 1000 m a.s.l., 15° 33.00' 12.18" N 121° 25.00' 21.85" E, *V. C. Linis 2881-07* (PNH); Mt. Hugis Balanga, Mingan Mountains, Aurora Province, Luzon Island, Philippines, on tree trunk, montane forest, November 25, 2007, 1300 m a.s.l., 15° 33.00' 18.00" N 121° 25.00' 46.30" E, *V. C. Linis 2911-07* (PNH); Mt. Hugis Balanga, Mingan Mountains, Aurora Province, Luzon Island, Philippines, on tree trunk, montane forest, November 25, 2007, 1300 m a.s.l., 15° 33.00' 18.00" N 121° 25.00' 46.30" E, *V. C. Linis 2942-07* (PNH); Mt. Hugis Balanga, Mingan Mountains, Aurora Province, Luzon Island, Philippines, on tree trunk, montane forest, November 25, 2007, 1300 m a.s.l., 15° 33.00' 18.00" N 121° 25.00' 46.30" E, *V. C. Linis 2943-07* (PNH).

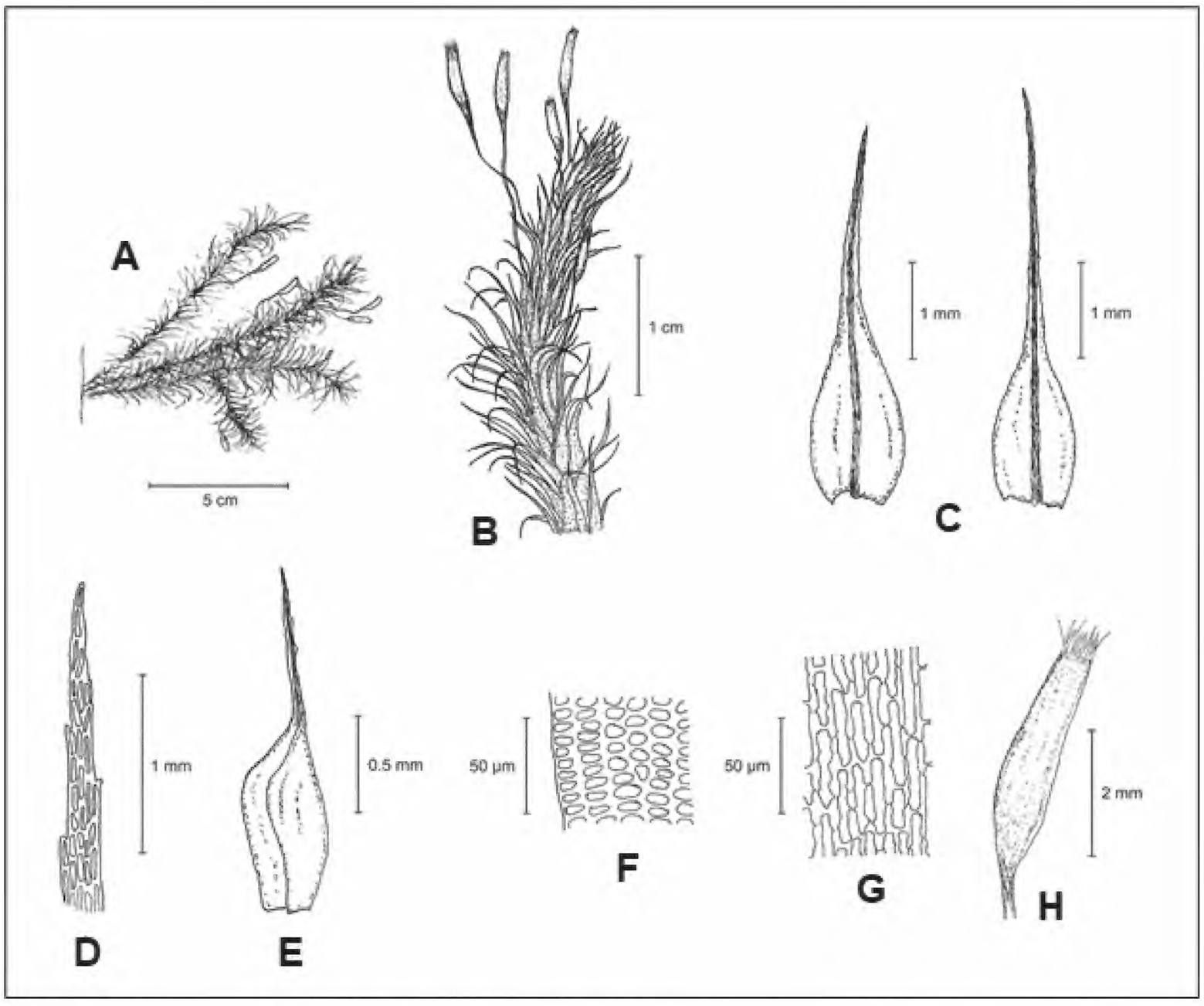

Fig. 6. *Bescherellia elegantissima* Duby. (A) Habit. (B) Portion of dry shoot. (C) Stem leaves. (D) Apex of leaf. (E) Inner perichaetial leaf. (F) Median laminal cells adjacent to margin of leaf. (G) Basal laminal cells near costa of leaf. (H) Capsule. (All from *Linis 2942-07* (PNH)).

Claopodium assurgens (Sull. & Lesq.) Cardot, *Bulletin de la Société Botanique de Genève* 3: 283. 1911. (Leskeaceae)

The moss identified as *C. assurgens* in Mingan Mountains (Fig. 7) is morphologically similar to other Asian materials examined (Gunung Halimun National Park, Java Island, Indonesia, *B. C. Ho 05314* (SIN); Mount Apo, North Cotabato Province, Mindanao Island, Philippines, *F. Schumm and U. Schwarz 4993* (SIN); Mount Iraya, Batan Island, Batanes Province, Philippines, *M. Suzuki 1794-b* (CAHP); Vũ Quang National Park, North Central Coast, Vietnam, *B. C. Tan 02-208* (SIN)). It is also superficially similar to its local congener, *C. prionophyllum*, but the latter is a larger plant (up to 10 cm long) bearing non-revolute stem leaves with tips abruptly narrowing into linear, slightly twisting acumen. The stem leaves found in *C. assurgens* are almost similar in shape but differ from *C. prionophyllum* in having revolute margins in the upper half with tips ending into non-twisting acumen. In *C. prionophyllum,* almost all leaf cells in its branch leaves except at the acumen bear papillae. These papillae are absent along the margins of branch leaves in *C. assurgens*.

Extra-Philippine Distribution: East Asia (Noguchi *et al.* 1991; Thin 1997; Wu *et al.* 2002) and in the island of Java, Indonesia (Fleischer 1915–1922). **Intra-Philippine Distribution:** Documented in Batan island (Tan and Iwatsuki 1983, 1991) and Mount Apo in Mindanao island (Tan *et al.* 2000). **Specimen examined:** Mt. Hugis Balanga, Mingan Mountains, Aurora Province, Luzon Island, Philippines, on wet rocks, montane forest, November 25, 2007, 1300 m a.s.l., 15° 33.00' 18.00" N 121° 25.00' 46.30" E, *V. C. Linis 2922-07* (PNH).

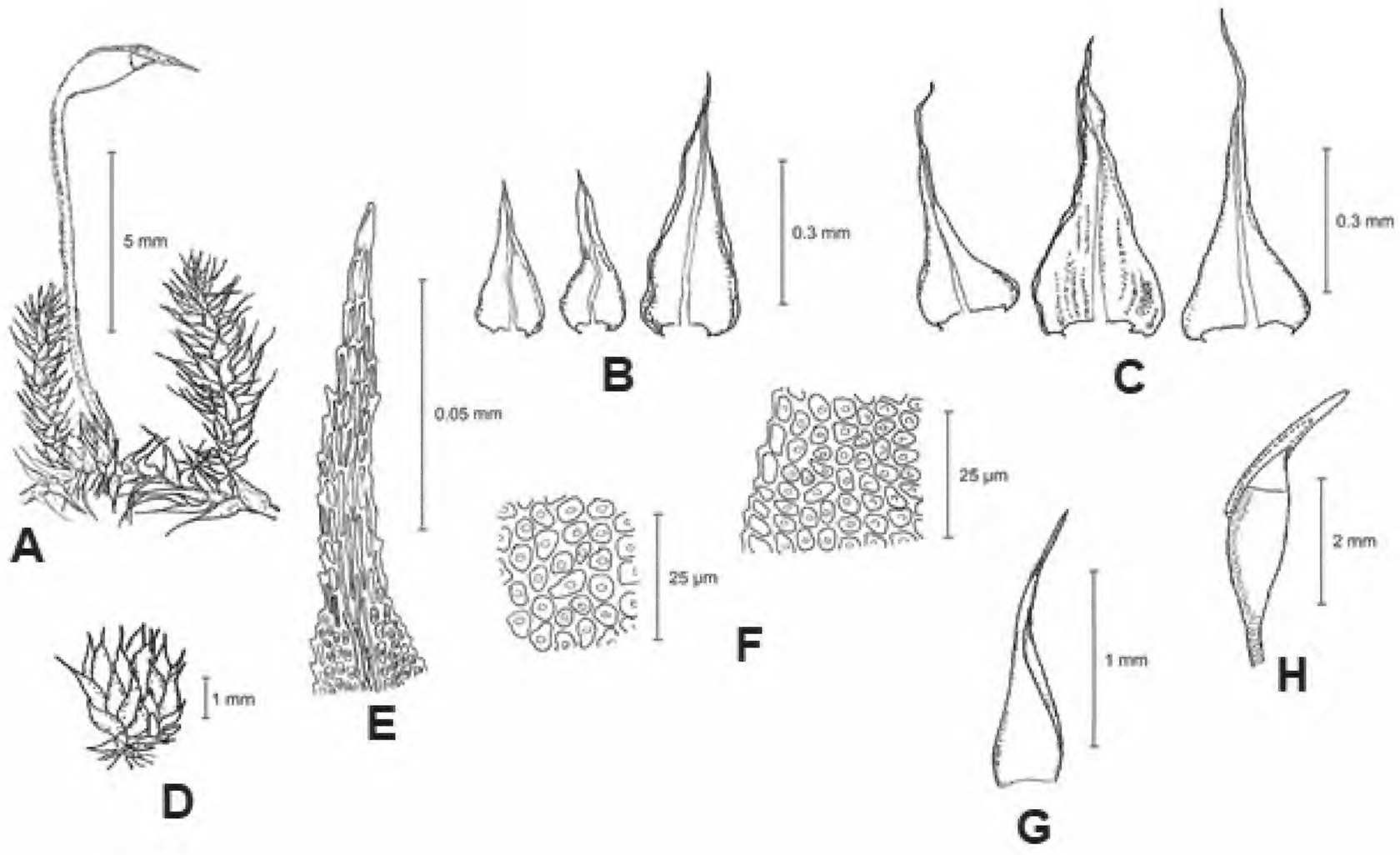

Fig. 7. *Claopodium assurgens* (Sull. & Lesq.) Cardot. (A) Portion of shoot. (B) Branch leaves. (C) Stem leaves. (D) Dwarf male plant. (E) Apex of branch leaf. (F) Median laminal cells of branch leaf. (G) Inner perichaetial leaf. (H) Capsule. (All from *Linis 2922-07* (PNH)).

Pseudoparaphysanthus moutieri (Broth. & Paris) S.Olsson, Enroth, Huttunen & D.Quandt. *Bryophyte Diversity and Evolution* 38(2): 64. 2016. (Neckeraceae)

Touw and Ochyra (1987) and Ochyra and Enroth (1989) placed *Neckeropsis moutieri* (Broth. & Paris) M.Fleisch. in *Neckeropsis* sect. *Pseudoparaphysanthus* based on morphological characters. Later, Olsson *et al.* (2016) transferred *N. moutieri* and several other species of *Neckeropsis* in the genus *Pseudoparaphysanthus* (Broth.) S.Olsson, Enroth, Huttunen & D.Quandt based on the molecular data used in their analysis. Based on this evidence, the author followed Olsson *et al.* (2016) in transferring *N. moutieri* to genus *Pseudoparaphysanthus*.

The Luzon material of *P. moutieri* has a very distinct and sharply demarcated limbidia along both leaf margins consisting of elongated, thick-walled cells reaching to leaf apex or nearly so which sets it apart from members of *Neckeropsis* (Fig. 8). In addition, the leaves of *P. mouteri* have either broadly acute or obtuse leaf apices, a very strong costa reaching to leaf apex or ending just a few cells below it and lack basal auricles. In the Philippines, *P. mouteri* can be confused with a similar rheophytic species *P. bonianus* (Besch.) S.Olsson, Enroth, Huttunen & D.Quandt. However, the latter species has limbidia consisting only of one layer of cells while that of *P. moutieri* consisted of 2 layers. Furthermore, the leaf margins of *P. moutieri* are densely denticulate to dentate throughout while the leaf margins of *P. bonianus* are denticulate only in the narrowed part of leaf apices or entirely absent.

Extra-Philippine Distribution: North Vietnam (Pócs 1969; Wu *et al.* 2011), southern China (Wu *et al.* 2011). **Intra-Philippine Distribution:** Mount Purog in Samar island (Touw 1972; Tan and Iwatsuki 1991). **Specimen examined:** North slope of Mount Isarog, Province of Camarines Sur, Luzon Island, Philippines, on stone beside a creek, May 13, 1991, *J. R. Cabalguinto 2107* (PNH).

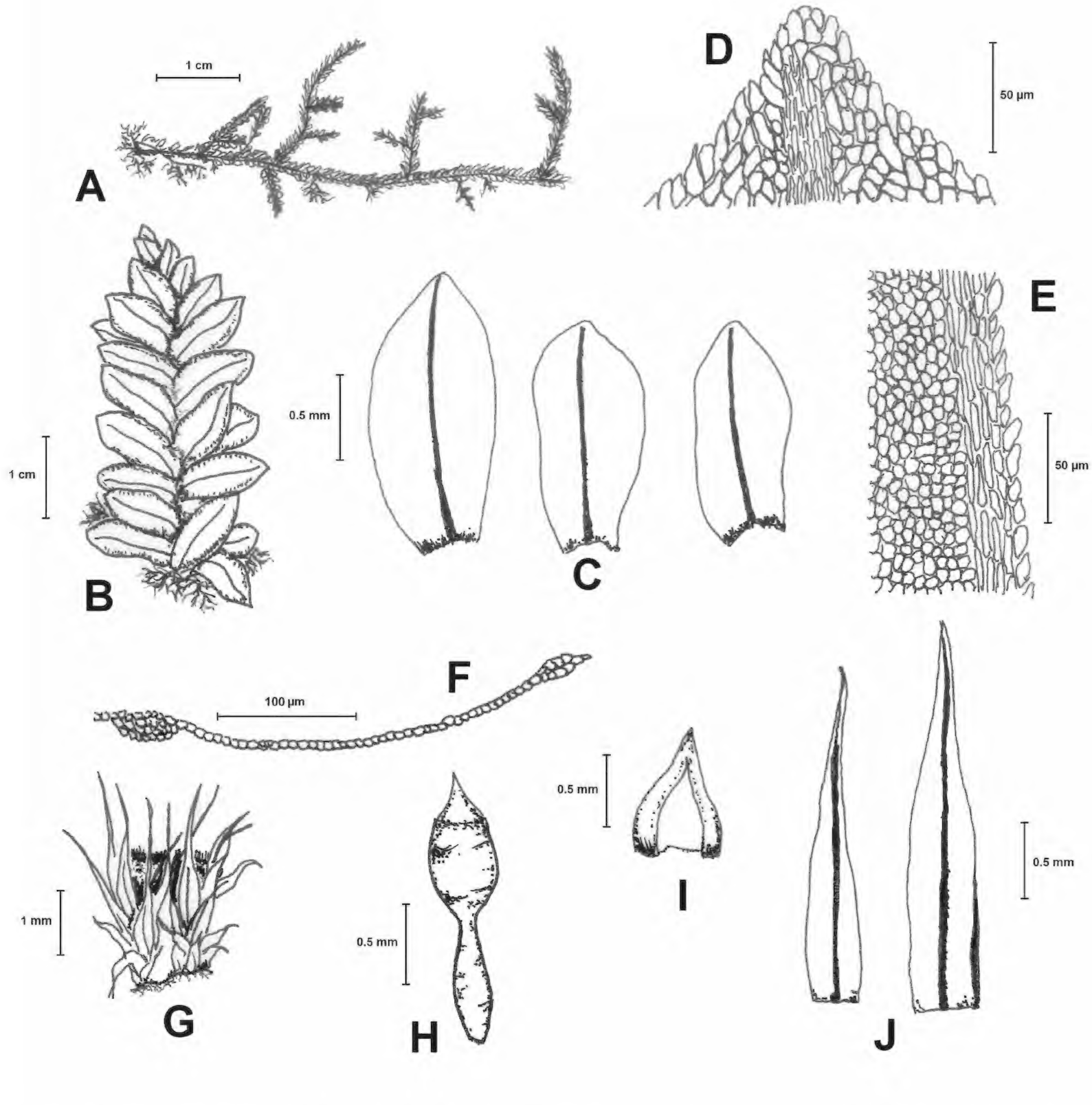

Fig. 8. *Pseudoparaphysanthus moutieri* (Broth. & Paris) S.Olsson, Enroth, Huttunen & D.Quandt. (A) Habit. (B) Portion of shoot. (C) Branch leaves. (D) Apex of branch leaf. (E) Margin of branch leaf showing the limbidium and lamina cells. (F) Cross-section of a branch leaf. (G) Perichaetium. (H) Capsule. (I) Calyptra. (J) Outer perichaetial leaves. All from *J. R. Cabalguinto 2107* (PNH).

Racopilum magnirete E.B.Bartram, *Farlowia* 1: 506, figs 11–14. 1944. (Racopilaceae)

The morphological characters of Luzon materials identified as *R. magnirete* (Fig. 9) agree well with van Zanten's (2006) description of the species based on the type material collected by Bartram (1944). Close examinations of Mingan specimens identified as *R. cuspidigerum* (Schwägr.) Ångstr. including a type of material (Hawaiian Islands, U.S.A., *C. Gaudichaud-Beaupré s.n.* (BM001109833)) revealed that *R. magnirete* is a small epiphytic plant with loosely inserted lateral leaves that spread sideway whereas for the slightly larger *R. cuspidigerum*, the lateral leaves are more closely inserted. In *R. magnirete*, the ovate lateral leaves have undulating lamina with margins becoming coarsely toothed toward the base of the costa. Similar leaves in *R. cuspidigerum* are more narrowly ovate in shape with margins either entire or serrated toward the leaf apices. If serrated, the teeth in *R. cuspidigerum* are composed mainly of single cells compared to the 2 or 3 cellular teeth in *R. magnirete* (van Zanten 2006). Given these circumstances, *R. magnirete* is treated here as a separate species apart from *R. cuspidigerum* for the time being, until a definite conclusion become available.

Extra-Philippine Distribution: British Solomon Islands (van Zanten 2006). **Intra-Philippine Distribution:** Mindanao (Bartram 1944; Tan and Iwatsuki 1991). **Specimen examined:** So. Siete, Mingan Mountains, Gabaldon, Nueva Ecija Province, Luzon Island, Philippines, on trunk of Aymit (*Ficus* sp.) tree, November 3, 2007, 460 m a.s.l., 15° 29.00' 21.58" N 121° 20.00' 48.79" E, *V. C. Linis 2734-07* (PNH); So. Siete, Mingan Mountains, Gabaldon, Nueva Ecija Province, Luzon Island, Philippines, on tree trunk, November 3, 2007, 460 m a.s.l., 15° 29.00' 21.58" N 121° 20.00' 48.79" E, *V. C. Linis 2738-07* (PNH); So. Siete, Mingan Mountains, Gabaldon, Nueva Ecija Province, Luzon Island, Philippines, on tree trunk, November 3, 2007, 460 m a.s.l., 15° 29.00' 21.58" N 121° 20.00' 48.79" E, *V. C. Linis 2746-07* (PNH); Brgy. Pantoc, Gabaldon, Nueva Ecija Province, Luzon Island, Philippines, on tree trunk, November 3, 2007, 615 m a.s.l., 15° 28.00' 27.63" N 121° 21.00' 49.76" E, *V. C. Linis 2750-07* (PNH).

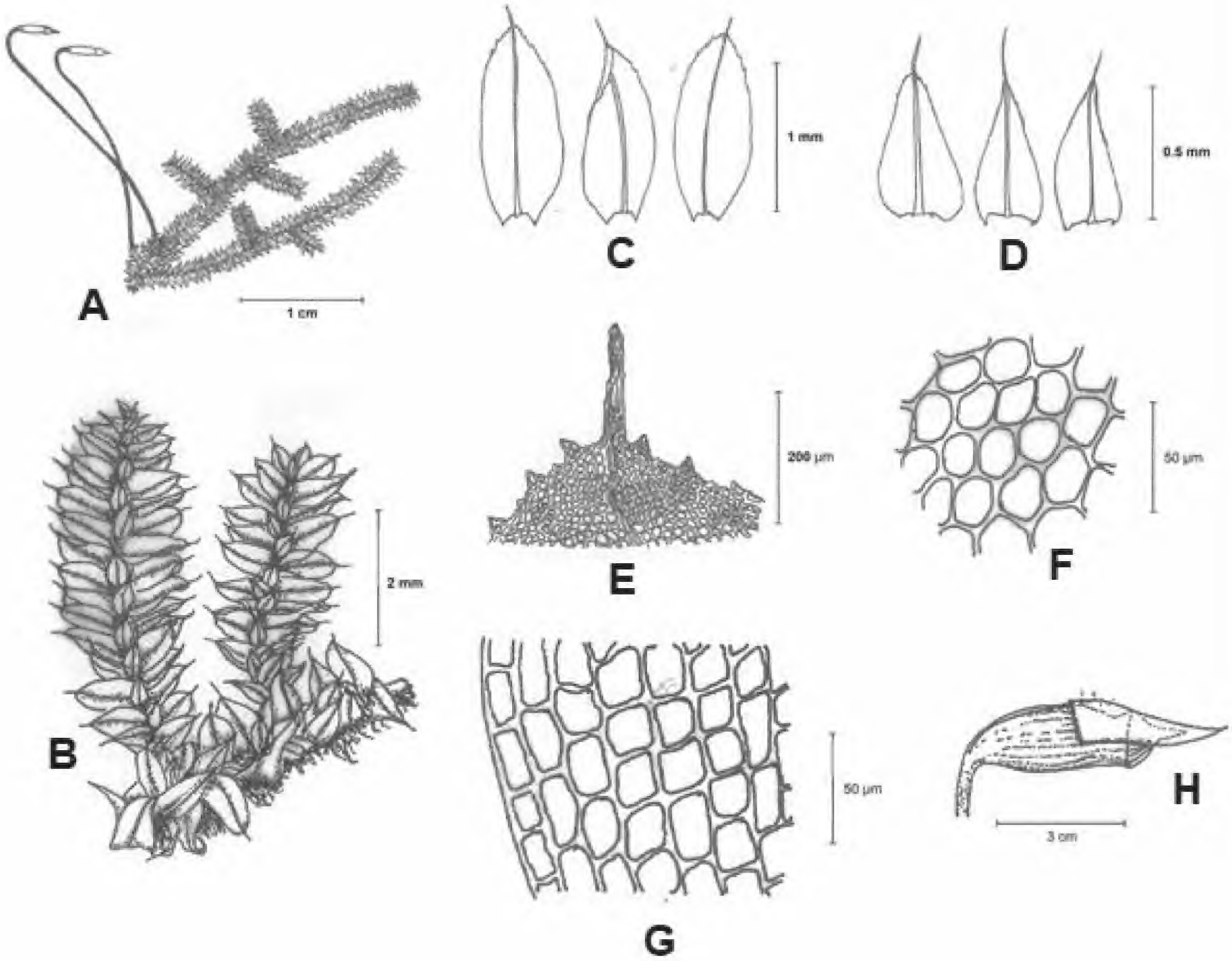

Fig. 9. *Racopilum magnirete* E.B.Bartram. (A) Habit. (B) Portion of shoot. (C) Lateral leaves. (D) Dorsal leaves. (E) Apex of lateral leaf. (F) Median laminal cells of lateral leaf. (G) Basal laminal cells adjacent to margin of lateral leaf. (H) Capsule. (All from *Linis 2746-07* (PNH)).

Conclusions

The updated distributional patterns exhibited by the nine reported Philippine mosses are significant and useful to the phytogeographical studies of Philippine moss flora. For instance, the additions of *Chaetomitrium horridulum*, *Chaetomitrium vrieseanum*, and *Dicranoloma deplanchei* for the Philippine moss flora further fortify its current relationship with neighbouring areas in the Malesian region whereas the report of *Anomodontopsis rugelii* is an addition to the growing country list of widespread northern latitude mosses, albeit, restricted to the high mountains of Luzon. The addition of previously unreported four Philippine mosses: *Anomodon pseudotristis*, *Bescherellia elegantissima*, *Claopodium assurgens*, and *Racopilum magnirete* to Luzon island, on the other hand, only goes to show that some Philippine moss species displaying disjunctive distributions within the archipelago could likely be a result of under-sampling in the intervening islands. These could also imply that species displaying similar distributions may eventually turn out to be Philippine-wide in distribution.

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References

Akiyama H (1997) Taxonomic studies of mosses of Seram and Ambon (Moluccas, East Malesia) collected by Indonesian–Japanese Botanical Expeditions VIII. Meteoriaceae, Hookeriaceae, and Trachypodaceae. *Natural Human Activity* 2: 9–31.

Akiyama H, Suleiman M (2001) Taxonomical notes on the genus *Chaetomitrium* (Hookeriaceae, Musci). *Hikobia* 13: 491–509.

Ariyanti NS, Gradstein SR, Sporn SG, Angelika R, Tan BC (2009) Catalogue of the bryophytes of Sulawesi, supplement 1: new species records. *Blumea* 54: 287–289. https://doi.org/10.3767/000651909X476300

Azuelo AG, Tan BC, Shevock JR, Manual A, Yorong A, Sariana L (2015) Mosses new for Mindanao Island, Republic of the Philippines. *Proceedings of the California Academy of Sciences* 62(4): 127–134.

Bartram EB (1939) Mosses of the Philippines. *Philippine Journal of Science* 68(1–4): 1–437.

Bartram EB (1944) New and noteworthy Philippine mosses. *Farlowia* 1(4): 503–513. https://doi.org/10.5962/p.315993

Brummitt RK, Powell CE (1992) *A list of authors of scientific names of plants, with recommended standard forms of their names, including abbreviations*. Kew: Royal Botanic Gardens.

Enroth J (1990) Bryophyte flora of the Huon Peninsula, Papua New Guinea. XXXVIII. Cyrtopodaceae and Cryphaeaceae (Musci). *Annales Botanici Fennici* 27: 177–188.

Fife AJ (2014) Anomodontaceae. In: Heenan PB, Breitwieser I, Wilton AD, editors. *Flora of New Zealand - Mosses*. Fascicle 9. Lincoln: Manaaki Whenua Press. (5 August 2014) [accessed 2019 December 11]. http://dx.doi.org/10.7931/J2JW8BS5

Fife AJ (2019) Dicranaceae. In: Smissen R, Wilton AD, editors. *Flora of New Zealand – Mosses*. Fascicle 42. Edition 2. Lincoln: Manaaki Whenua Press. (21 February 2019 Second edition) [accessed 2021 October 21]. http://dx.doi.org/10.7931/B1Y026.2

Fleischer M (1906–1908) *Die Musci der Flora von Buitenzorg*. Vol. 3. Leiden: EJ Brill.

Fleischer M (1915–1922) *Die Musci der Flora von Buitenzorg*. Vol. 4. Leiden: EJ Brill.

Goffinet B, Buck WR, Shaw AJ (2009) Morphology, anatomy, and classification of the Bryophyta. In: Goffinet B, Shaw AJ, editors. *Bryophyte Biology*. Cambridge: Cambridge University Press; pp. 55–138.

Granzow-de la Cerda Í (1997) Revision and phylogeny of *Anomodon* and *Herpetineuron* (Anomodontaceae, Musci). *Contributions from the University of Michigan Herbarium* 21: 205–275.

Ignatov MS, Fedorova AV, Fedosov VE (2019) On the taxonomy of Anomodontaceae and *Heterocladium* (Bryophyta). *Arctoa* 28(1): 75–102. https://doi.org/10.15298/arctoa.28.08

Klazenga N (1999) A revision of the Malesian species of *Dicranoloma* (Dicranaceae, Musci). *Journal of the Hattori Botanical Laboratory* 87: 1–130.

Linis VC (2004) A checklist of Mosses in Mt. Arayat, Pampanga, Philippines. *Journal of Tropical Biology* 3: 2–6.

Linis VC (2006) A review of intra-Philippine distribution pattern of Philippine mosses based on recent evidence of tectonic evolution of the archipelago: insights and problems. *Banwa* 3(1&2): 31–64.

Linis VC (2009) Biogeography of Mindoro mosses. *Blumea* 54: 290–296. https://doi.org/10.3767/000651909X476319

Linis VC (2010) The moss flora of Camiguin Island, Philippines, and their floristic relations to adjacent islands in the archipelago. *Telopea* 12(4): 525–542. https://doi.org/10.7751/telopea20105844

Linis VC (2014) Biogeographical notes on the moss floras of Bicol Peninsula in Luzon and the Catanduanes Islands, The Philippines. *Philippine Journal of Science, Special Issue* 142: 119–133.

Linis VC (2018) A new country record and additions to the moss floras of Luzon and Mindanao islands, Philippines. *Telopea* 21: 91–99. https://doi.org/10.7751/telopea12512

Linis VC (2019a) Notes on the diversity and floristic affinity of mosses (Musci, Bryophyta) from Zambales Mountain Range, Luzon island, Philippines. *Phytotaxa* 388(1): 69–97. https://doi.org/10.11646/phytotaxa.388.1.3

Linis VC (2019b) New Philippine moss records for Luzon and Mindanao islands. *Journal of Bryology* 41(1): 48–58. https://doi.org/10.1080/03736687.2018.1560542

Linis VC, Tan BC (2008) Progress of studies on phytogeography and biodiversity of Philippine moss flora from 1991 to 2006. In: Mohamed MAH, Baki BB, Nasrulhaq-Boyce A, Lee PKY, editors. *Bryology in the New Millennium*. Kuala Lumpur: University of Malaya; p. 13–22.

Linis VC, Tan BC (2010) Eleven new records of Philippine mosses. *Acta Bryolichenologica Asiatica* 3: 95–100.

Linis VC, Tan BC (2013) Eight additional new records of Philippine mosses. *Telopea* 15: 45–49. https://doi.org/10.7751/telopea2013006

Lubos, L (2010) Species richness, distribution, and status of mosses in selected mountains in Mindanao, Philippines. *Asian Journal of Biodiversity* 1(1): 72–90. https://doi.org/10.7828/ajob.v1i1.103

Noguchi A, Iwatsuki, Z, Yamaguchi T (1991) *Illustrated moss flora of Japan*. 4. Nichinan, Miyazaki, Japan: Hattori Botanical Laboratory; pp. 743–1012.

Ochyra R, Enroth J (1989) *Neckeropsis touwii* (Musci, Neckeraceae), new species from Papua New Guinea, with an evaluation of sect. *Pseudoparaphysanthus* of *Neckeropsis*. *Annales Botanici Fennici* 26: 127–132.
Olsson S, Enroth J, Huttunen S, Quandt, D (2016) Phylogeny of *Neckeropsis* and *Himantocladium* (Neckeraceae, Bryophytina). *Bryophyte Diversity and Evolution* 38(2): 53–70. https://doi.org/10.11646/bde.38.2.4
Pócs T (1969) Fifth contribution to the bryoflora of North Vietnam. *Botanikae Közlemények* 56: 139–147.
Pursell, RA, Reese, WD (1982) The mosses reported from New Caledonia. *Journal of the Hattori Botanical Laboratory* 53: 449–482.
Sastre-de Jesús I (1987) Revision of the Cyrtopodaceae and transfer of *Cyrtopodendron* to the Pterobryaceae. *Memoirs of The New York Botanical Garden* 45: 709–721.
Shevock JR, Yorong AP (2018) New additions to the moss flora of Mindanao island, Republic of the Philippines. *Philippine Journal of Systematic Biology* 12: 68–72. https://doi.org/10.26757/pjsb.2018a12004
Suleiman M, Akiyama H (2014) Malesian *Chaetomitrium* (Symphyodontaceae, Musci): type illustrations, taxonomical notes, and key to the species. *Humans and Nature* 25: 1–62. https://doi.org/10.24713/hitotoshizen.25.0_1
Suleiman M, Anwar I (2021) *Chaetomitrium vrieseanum* Bosch & Sande Lac. (Symphyodontaceae), a noteworthy record of a moss from Borneo. *Check List* 17(1): 227–231.
Tan BC (1987) New records of Philippine mosses. *Memoirs of The New York Botanical Garden* 45: 446–454. https://doi.org/10.15560/17.1.227
Tan BC, Iwatsuki Z (1983) Nineteen new records of Philippine mosses. *Kalikasan, Philippine Journal of Biology* 12: 328–350.
Tan BC, Iwatsuki Z (1991) A new annotated Philippine moss checklist. *Harvard Papers in Botany* 3: 1–63.
Tan BC, Lubos L, Schwarz U (2000) New and biogeographically noteworthy records of Philippine mosses from Mindanao Island. *Tropical Bryology* 18: 27–37. https://doi.org/10.11646/bde.18.1.5
Tan BC, Robinson H (1990) A review of the Philippine Hookeriaceous taxa (Musci). *Smithsonian Contribution to Botany* 75: 1–41. https://doi.org/10.5479/si.0081024X.75
Tan BC, Shevock JR (2014) Noteworthy mosses collected from the 2014 expedition of CAS and CMU new to Mindanao Island of the Philippines. *Bryophyte Diversity & Evolution* 36: 22–30. https://doi.org/10.11646/bde.36.1.2
Tan BC, Shevock JR (2015) Species of *Macromitrium* (Orthotrichaceae) new to the Mindanao region and the Philippines with one species new to science. *Proceedings of the California Academy of Sciences* 64: 541–549.
Tan BC, Shevock JR, Coritico F, Amoroso V (2015) Mosses new for Mindanao Island, The Philippines III. *Bulletin of the National Museum of Nature and Science, Series B (Botany), Tokyo* 41: 91–97.
Thin, NN (1997) The vegetation of Cucphuong National Park, Vietnam. *Sida, Contributions to Botany* 17(4): 719–759.
Thouvenot L, Bardat J (2013) Contribution to the bryophyte flora of New Caledonia. I. New taxa and amendments. *Cryptogamie, Bryologie* 34(1): 37–47. https://doi.org/10.7872/cryb.v34.iss1.2013.37
Touw A (1972) Additional notes on *Neckeropsis*. *Lindbergia* 1: 184–188.
Touw A, Ochyra R (1987) Additional notes on *Neckeropsis* 2. *Lindbergia* 13: 97–104.
van Zanten BO (2006) A synoptic review of the Racopilaceae (Bryophyta, Musci). 1. Asian, Pacific, and Australasian species of the genus *Racopilum*. *Journal of the Hattori Botanical Laboratory* 100: 527–552.
Wu P-C, Crosby MC, He S (2002) Hookeriaceae–Thuidiaceae. In: He S, editor. *Moss flora of China*. Vol. 6. Beijing, New York & St. Louis: Science Press & Missouri Botanical Garden.
Wu P-C, Crosby MC, He S (2011) Erpodiaceae–Climaciaceae. In: He S, editor. *Moss flora of China*. Vol. 5. Beijing, New York & St. Louis: Science Press & Missouri Botanical Garden.

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Nomenclatural notes on New South Wales flannel flowers (*Actinotus* spp., Umbelliferae/Apiaceae) and Leopold Trattinnick's other Australian plant-names

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Abstract

After a thorough consideration of the history of the European collection and subsequent early cultivation of the commercial flannel flower, lectotypes are designated for *Actinotus helianthi* Labill., *Eriocalia major* Sm. (i.e. *A. helianthi*) and *E. minor* Sm. (i.e. *A. minor* (Sm.) Tratt., the first publication of which is revealed). Other neglected names coined by Trattinnick, including generic ones, applied to Australian and other plants, and published on (generally) plagiarised plates, are discussed and disposed of. One such plate is a copy of the iconotype of *Amaryllis* × *johnsoniana* Ker Gawl., providing an earlier specific epithet for *Hippeastrum* × *johnsonii* (Gowen) Herb. (Amaryllidaceae), a bulbous plant long cultivated in Australia and whose name should be conserved with the later spelling; a synonym, *Amaryllis* × *carnarvonia* DC. is lectotypified. Attention is drawn to confusions in localities on labels attached to specimens of species (in various families) collected on both D'Entrecasteaux's and Baudin's voyages to Australia.

Actinotus helianthi

Although herbarium material of the now commercially cultivated flannel flower (*Actinotus helianthi* Labill., Umbelliferae/Apiaceae) was collected by Joseph Banks and Daniel Solander at Botany Bay during their first landfall in Australia between 28 April and 5 May 1770, it took more than three decades before the species received a scientific name. Specimens gathered by them in 1770 survive in the Natural History Museum London (BM013717918) with duplicates in the National Herbarium of New South Wales (NSW133494) and the Muséum national d'Histoire naturelle in Paris (P03223682; accessioned 17 November 1911), while the field sketch by Sydney Parkinson, as well as the finished drawing by John Fredrick Miller dated 1774 based on it, are both at BM (Henderson 1983: 152; Diment et al. 1984: 91; Mabberley 2019: 31).

Subsequently, under Banks's auspices, Gabriel Smith produced an engraved copper plate, also at BM, but, perhaps because of the cost of Banks's *Endeavour* Florilegium project, no proper publication of Parkinson's illustration took place until 1901 (Diment et al. 1984: 12–14, 91; Mabberley 2017: 166–67, 2020a: 46–48, 69).

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However, in 1800, an image of *Actinotus helianthi* labelled 'Sun Flower of New South Wales' was published in England (Mabberley 2020a: 90), but that illustration was not accompanied by a scientific name.

Geographical inconsistencies

The binomial *Actinotus helianthi* appeared first in *Novae Hollandiae plantarum specimen* (1804–1807) of Jacques-Julien Houtou de La Billardière (Labillardière; 1775-1834) with description (p. 67) and plate (t. 92), published simultaneously in September 1805[i]. However, there are geographical anomalies associated with this taxon (Nelson 1974, 1975; Mabberley 2020a: 152): firstly, Labillardière gave 'Terra Van Leeuwin' as its locality, that is Western Australia, where the species is not known to occur, and, secondly, the plant is naturally restricted in distribution to what is now New South Wales and Queensland, regions neither Labillardière nor any other member of the expedition (1791–93) led by Antoine Raymond Joseph de Bruni d'Entrecasteaux (1737–93) is known to have visited. Labillardière must have added an incorrect locality to his account.

Before sailing to Australia, Labillardière had worked in Banks's herbarium 1783–85 (Mabberley 2020a: 145) so it is possible he saw Banks' and Solander's *Actinotus* specimens, but no record of this has been found. It is conceivable that Labillardière's generic description was made from a species he could have encountered in Western Australia, e.g. *Actinotus leucocephalus* Benth., but no herbarium specimens of the species native there survive in his herbarium now at FI, though, clearly, the plate must have been drawn from material Labillardière did not collect in Australia.

The only vaguely germane specimen at FI is from René Desfontaines's herbarium (FI059398) with a label in the latter's hand (M. Callmander, pers. comm., 1 October 2021). It bears Labillardière's binomial and place of publication, besides Étienne Pierre Ventenat's unpublished name 'Actinodes artemisiaefolia' (see below) and James Edward Smith's *Eriocalia major* of 1806, so at least the last name must have been added to the sheet after Labillardière's publication. Another specimen with these three names on a label, all in the hand of Desfontaines, is in Paris (P00270102) with, significantly, 'Actinodes artemisiaefolia' followed by the note 'Vent. malm.', and the locality 'Port Jackson' (see below).

Nelson (1975) compared a specimen (G0035933) in Ventenat's herbarium in Geneva with Labillardière's plate, but pointed out that the annotations with it could not be definitely said to be in Labillardière's hand. The present authors attribute the long manuscript description now attached to the sheet to Ventenat himself (cf. Burdet 1979), though the note on the accompanying label 'Nlle Hollande. M. Labillardiere' is in another, so far unidentified hand. Nonetheless, Nelson annotated this specimen 'probably HOLOTYPE of *Actinotus helianthi* Labill. not collected by Labillardière'. However, as there is no evidence that Labillardière collected this specimen or wrote on this sheet while the hitherto unconsidered annotation in Ventenat's hand on this sheet has 'Nous avons décrit le genre très différemment' [we have described this genus quite differently], G0035933 cannot be type material. For further discussion of this specimen see below.

Investigation

A search was therefore undertaken in herbaria known to hold material collected by Labillardière during the D'Entrecasteaux expedition, namely B-W, FI, G, P and elsewhere, but this yielded no *Actinotus* specimens annotated by Labillardière indicating that they were collected by him in Australia. Specimens on sheet KFTA0000083 (Kirov Forestry Academy, Saint Petersburg, Russia: three fragments with labels, one annotated capsule, one unannotated) have neither Labillardière annotations nor any locality information beyond 'Nov. Holl.'. Two specimens in Geneva, i.e. G0066129 and G00661231 are labelled 'côte orient.' and 'detr, d.'Entre.' respectively and came to Augustin Pyramus de Candolle from the Muséum in 1821. No collectors are indicated and both localities on them are incorrect.

In general, Labillardière seems to have failed to record even generalised localities in the field: in his preliminary manuscript descriptions added to his collections of Umbelliferae/Apiaceae at FI there is no locality information at all. His specimens sent to P may thus have had no locality information. The only sheet with notes, almost certainly in Labillardière's hand (P-JU No. 10408, left hand specimen), has 'Actinotus LaBillard.' and the locality 'Detroit dentecastaux' [sic; D'Entrecasteaux], that is Tasmania (where it does not grow), with, in Jussieu's hand (M. Callmander, pers. comm. 1 October 2021), 'helianthi n. holl. t. 92, Nou. Hollande' and 'Herb. du Muséum 1815' added, the latter date apparently being the year of acquisition. In parallel with this, Lamarck, Encycl. 8: 336 (1808) initially quoted Labillardière's original Western Australian locality but later Jean Louis Marie Poiret changed it to 'le Cap Van Diemen', i.e. Tasmania, in Lamarck's Tableau 3: 589 (1823).

Leschenault de la Tour and/or Robert Brown?

Nelson (1975), followed by Duyker (2003: 232), suggested that Labillardière's material was perhaps collected on Baudin's expedition by Jean-Baptiste Leschenault de la Tour (1773–1826) when in New South Wales. There

he met Robert Brown and they collected plants together, as on 11 May 1802 (Mabberley 1985: 94–95; Vallance et al. 2001: 203).

According to Brown's descriptive slips at BM (Brown MSS B. 65 25/156), Brown collected *Actinotus helianthi* on 17 May 1802, making a description two days later, adding to it Solander's unpublished name *Involucrata candida*. It is conceivable that Brown shared his collection (now Iter Austral. 4508) with Leschenault, but there is no Leschenault specimen at P (but see below) and specimens of *A. helianthi* collected by Brown were apparently accessioned in P only much later – P03223692 and P03223717 from K on 19 January 1884, P03223691 and P03223698 from E on 28 May 1890.

According to his descriptive slips B.65 25/153–154, Brown proposed naming the plant *Patersonia* after Capt. William Paterson (1755-1810), who not only supplied seeds of many New South Wales plants to the English nursery firm of Lee and Kennedy (see below) from as early as 1791 (Mabberley 2020a: 81) but also, perhaps more than coincidentally, has been considered to be the possible source leading to the published illustrations that included 'The Sun Flower…' (Mabberley 2020a: 91). No doubt finding that Labillardière had published *Actinotus* for this new genus whilst Brown was sailing from Port Jackson [now Sydney] to Liverpool, Brown on his return recycled the name, giving it to a new genus of Iridaceae (*Patersonia* R.Br. of 1807), which stands today.

At P there are eleven specimens of *Actinotus helianthi*, mounted on five sheets (P00270103 left hand specimen, P00270104, P00270105, P00270106, P04330868), with printed labels reading 'Nouvelle Hollande, Côte méridionale, Voyage aux Terres-Australes. Capitaine Baudin. 1801', but without the name of any collector. The locality information is incorrect, since *A. helianthi* does not grow along the southern coast of Australia, but the material may have been collected by Leschenault, although this is nowhere mentioned. Another, perhaps parallel, example is that of the Australian pitcher-plant, *Cephalotus follicularis* Labill. (Cephalotaceae), which Leschenault certainly collected in Western Australia in February 1803 (G holo; G00176809, while Brown had already done so there in January 1802 [Brown 1832], these being the first two European gatherings), but, intriguingly, not even Leschenault was acknowledged in Labillardière's publication. This scarcely accords with Aimé Bonpland's assertion that Labillardière 'never looked at other herbaria, because he allowed no-one to look at his' (Mabberley 1985: 195). A sixth P sheet (P04330836) of *Actinotus helianthi* has three elements (the middle one fasciated), again without a collector's name but with a printed label, 'Côte orientale Baudin 1801', which does fit the known general geographical distribution of *A. helianthi* but could perhaps be Leschenault's (or even material given to him by Brown).

Other troubling localisations include the case of another member of Umbelliferae/Apiaceae, *Azorella lanceolata* Labill. (today's *Platysace lanceolata* (Labill.) Druce). It occurs only on the east coast of Australia (but not Tasmania) whereas the type locality is given as 'Terre van-Leuwin [Western Australia]' (Labillardière 1804–7: 74) though the specimen, P00270083, has the locality 'Detr D'Entrecasteau [Tasmania]' on the label. In completely different families (see also Nelson 1974, 1975), similar confusion obtains: the lectotype of *Nemedra elaeagnoidea* A. Juss. (today's *Aglaia elaeagnoidea* (A. Juss.) Benth., Meliaceae), a tropical species collected on Baudin's voyage, bears a printed label with 'Ile St Francois', i.e. St Francis Is., Nuyts Archipelago, South Australia (Mabberley 1988: 75); the locality of *Eucalyptus ovata* Labill. (Myrtaceae) is given as what is now Western Australia, but the tree is restricted to the south-east of the continent, including Tasmania, where Labillardière himself collected it (Mabberley 2020a: 152); the type specimen of *Persoonia saccata* R.Br. (Proteaceae) collected on Baudin's voyage is labelled 'Sharks Bay', i.e. 600 km north of the known distribution, within which native range the expedition is known to have collected plants in general (Weston 1994).

It is unlikely that such localities were added to deliberately mislead as part of some kind of 'commercial in confidence' ruse, so it has to be concluded that, upon being accessioned at P, printed labels were rather carelessly attached to specimens collected during both the D'Entrecasteaux and the Baudin voyages, leading to the nonsensical localisations burdening the literature - though this does not fully explain all of Labillardière's errors and omissions. In his defence, it must be borne in mind that his own collection was taken from him in Java, the "twenty-two biscuit cases, completely filled with dried plants with descriptions and observations….. noted in abbreviated form which he alone understands, and which remind him of an infinity of things which can only respond to his memory" being confiscated by the British and passed to Queen Charlotte (Stafleu 1967: Duyker 2003: 207–211, 224; Mabberley 2020a: 150). Only in 1796, through the good offices of Joseph Banks, were they restored to Labillardière, but their condition by then is unrecorded.

On the other hand, the apparently blatant non-acknowledgment of Leschenault's work may well reflect other prevailing attitudes and prejudices (cf. Mabberley 2020b). Leschenault was on 'the opposite side' from 'citoyen' (originally bourgeois) Labillardière with his fervent attachment to the French Revolution (Jeandet 1883, Stafleu 1966, Chevalier 1953, Duyker 2003). Leschenault, with his noble father and brother, was imprisoned during the Reign of Terror in 1793, following the promulgation of the 'Loi sur les Suspects' and was released

only after the death (1794) of Robespierre; the Leschenault family fortunes were restored only with the return of the Bourbon monarchy in 1814. Moreover, unlike the unbending and reportedly misanthropic Labillardière (Chevalier 1953, Stafleu 1966, Duyker 2003: 232), the gregarious Leschenault, despite his background, was pliant enough to get support from Napoléon Bonaparte in the form of being appointed a member of Baudin's team – long before the Bourbon Restoration.

Cultivated in France?

Ventenat's manuscript note now attached to G0035933 (see above) suggests that he intended to describe as a new species the material he had before him. Indeed, several more specimens of *Actinotus helianthi* are known with the annotation '*Actinodes artemisiaefolia* Vent.', e.g. P-JU No. 10408, central specimen, with the note 'An 5 [1805] jard[in]. de malm[aison].' in Ventenat's hand; P03223718 has the annotation 'Actinotus Helianthi. La Bill. Nov. Holl. t. 92. Actinodes artemisiaefolia Vent. Malm.' in an unknown hand, while P03223677 has 'Vent. hort. Malm.'. Perhaps significantly, a pencil sketch has been attached to P03223718, showing the central flower head and the details 1, 3, 4 and 6 of plate 92 of the *Novae Hollandiae plantarum specimen*. This drawing is annotated 'LaBill. Nov. Holl. fasc. t. 92 Actinotus Helianthi' in an unknown hand and may have been made by Pierre-Antoine Poiteau (see below) or merely copied by another hand from Poiteau's published plate in Labillardière's book. The text on the verso of the pencil sketch is a brief description ending with the note 'LaBill. pag. 67'. Significantly, G0035933 (see above) also bears the name 'Actinodes Artemisaefolia Vent.' and is likely a duplicate of P-JU No. 10408, central specimen (M. Callmander, 1 October 2021, pers. comm.). Although the specimen in Geneva bears no reference to Malmaison, it is possible that this specimen was cultivated in the garden there.

Ventenat had been commissioned to describe plants cultivated in Joséphine Bonaparte's garden at Malmaison in what is now a western suburb of Paris (Callmander et al. 2017). This resulted in the publication of his *Jardin de la Malmaison* (1803–05) where several new or rare plants cultivated there were described by Ventenat. However, neither in this nor in any other work did Ventenat validate his '*Actinodes artemisiaefolia*', likely because Labillardière had beaten him to it by publishing his *Actinotus helianthi* in September 1805. On the other hand, Ventenat beat Labillardière with another plant: *Callistachys elliptica* Vent. predates *Gompholobium ellipticum* Labill. (i.e. *Oxylobium ellipticum* (Vent.) R.Br., Leguminosae/Fabaceae; Chappill et al. 2008).

Several nurseries are known to have supplied plants to Joséphine's gardeners as well as to the Jardin des Plantes in Paris, pre-eminent among them being Lee & Kennedy (Willson 1961), a London firm for which Joséphine was one of its most indulgent customers (Mabberley 2020a: 163). Despite hostilities between France and Britain during the Napoleonic period, Lee & Kennedy, besides the botanist James Edward Smith, the English patrons Aylmer Bourke Lambert, Charles Greville and Emperor Woodward (who had his own collector in New South Wales – Letouzey 1989: 603), as well as other nurserymen like William Forsyth and Daniel Grimwood, continued to be important sources of Australian novelties as seeds or plants for the French (Mabberley 2020a: 140). It is not impossible that, through one or more of them, living material (plants or seeds) of *Actinotus helianthi* reached Paris. It may indeed not be entirely coincidental that in England the plant had been called 'sun flower', as if *Helianthus*, and thus received the specific epithet '*helianthi*' conceivably associated with plants or seeds exported from England – but the name was to be validly published only in France.

However, there is no hard evidence that *Actinotus helianthi* was in cultivation in England by then and it is not listed in W.T. Aiton's *Hortus kewensis* (1810–13) or Robert Sweet's *Hortus suburbanus londinensis* (1818). Friedrich Dietrich, *Nachträge zum Vollständigen Lexicon der Gärtnerei und Botanik*. 3: 218 (1817) pointed out that it was not then being grown in Germany or anywhere on the Continent (but see below). By the 1820s (see Edwards, *Botanical Register* 8: t. 654, 1822), though, the name *Actinotus helianthi* was certainly being applied to the Port Jackson (New South Wales) plant reportedly being newly grown in England, where it had first been called *Eriocalia major*, now with the latter name correctly in synonymy, apparently for the first time.

If Labillardière's material did not come from the British, could it have been collected by one of the gardeners of the Baudin expedition in Australia? When *Naturaliste* arrived at Le Havre (Normandy, France) on 7 June 1803, André Thouin, professor of horticulture at the Muséum, was sent there to take care of the botanical collections destined for his institution. However, he was also instructed to let Joséphine have any material her gardeners requested (see letter of Minister Chaptal to the professors of the Muséum dated 13 June 1803; Jouanin 1997). When the second frigate, *Géographe,* arrived at Lorient (Brittany, France) on 25 March 1804, the same applied to Geoffroy Saint-Hilaire, professor of zoology at the Muséum, dealing with the biological collections. Again, the plant materials were split between

the Muséum and Malmaison (Jouanin 1997). Specimens of *Actinotus helianthi* could thus have been simultaneously supplied to both (and subsequently cultivated in) Malmaison and the Jardin des Plantes in Paris. Evidence for the latter is found on a sheet of *Actinotus helianthi* (P-JU No.10408); the righthand specimen has a scarcely decipherable, miniscule note in Jussieu's hand, 'in hort mus paris 1805' [in the garden of the Muséum in Paris 1805].

Labillardière, associated with the Muséum, and Ventenat with Malmaison have been regarded as rivals. The Linnaean Desfontaines was Labillardière's champion, Jussieu, revivor of the Natural System, Ventenat's, in this 'long-time split' in Paris botany (Stafleu 1966; see also Duyker 2003: 227, 233), in other words the same tension as was that shortly afterwards between Karl Sprengel and Friedrich Dietrich in what is now Germany (Mabberley 2020b). This would help explain why Labillardière and Ventenat worked independently on these Australian plants - and in a competitive way.

It seems implausible that participants of the D'Entrecasteaux expedition, like the gardener Félix Delahaye (de Lahaye, de Lahaie, Lahaie; 1767-1829; Duyker 2003, 2005) or Louis Ventenat (1765-1794; Duyker 2000) played any part in the successful introduction of *Actinotus helianthi*, as their seed collections would have long lost their capacity to germinate. However, Delahaye became gardener to Joséphine, firstly at the Trianon (Versailles), then at Versailles itself and eventually at Malmaison in 1805 (Stafleu 1966: xxxi; Letouzey 1989: 228; Duyker 2005; Mabberley 2020a: 143).

Perhaps through Delahaye, though more likely from the Jardin des Plantes, living material of *Actinotus helianthi* could have reached Labillardière, who then would have prepared, based on it, a specific description and added the illustration (by Pierre-Antoine Poiteau [1766–1854], working as a freelance illustrator in Paris) in his *Novae Hollandiae plantarum specimen*. This is not entirely impossible since, for example, a specimen of *Callistachys lanceolata* Vent. (Leguminosae/Fabaceae), reportedly raised from seeds brought back from the Baudin expedition, was described as new to science in the last fascicle of *Jardin de la Malmaison* and illustrated there (Ventenat 1803–1805: t. 115). This fascicle appeared in November 1805, just two months after Labillardière had published *Actinotus helianthi* in his *Novae Hollandiae plantarum specimen*. Plants of *Actinotus helianthi* in Australia can produce flowers in as little as eight months from seed (Worrall et al. 2004), but seed viability is reported to be low after 153 days (Emery et al. 2017). *Naturaliste* with Baudin expedition collections left Sydney on 18 November 1802, reaching France in June 1803, so that it is just conceivable that some seeds survived the voyage, the resultant plant(s) flowering in Paris – to be drawn, but then die out completely soon afterwards. The right-hand specimen of P-JU No. 10408 (see above) with the correct locality information 'Port Jackson' seems to accord with this possible sequence of events.

The Baudin expedition had five gardeners (Jones 2017), but which of them could or might have collected material of *Actinotus helianthi* is impossible to say. Lists of plant material collected in Australia by one of them, Anselme Riedlé [Anselm Riedle], who died in Timor, survive (MNHN Paris, BC, MS 1685) as do reports by another gardener, Antoine Guichenot [Guichenault; Nelson 1976] who, when about to leave Port Jackson, listed on 9 November 1802 (MNHN, BC, MS THO273) two boxes of seeds. But, tantilisingly, there is no evidence that seeds of *Actinotus helianthi* were in those boxes. Moreover, in neither FI nor P is there any trace of Poiteau's drawing, which might have had annotations linking it to living material grown in France.

Conclusion

By comparison with the perpetrators of the geographical confusions above, Friedrich Dietrich (1817: 218) had the correct geography (but placed *Actinotus helianthi* (1805) in the synonymy of *Eriocalia major* Sm. (1806), following J.E. Smith in Rees, *Cyclopaedia* 13, 2 (26) Eriocalia (1809), who had considered *Actinotus* inadmissible, as the name was earlier used in mineralogy for what is now actinolite [including nephrite and a form of asbestos]). Smith's *Eriocalia major* was based on specimens and a drawing sent from Port Jackson by Surgeon John White of the First Fleet, besides the published plate by James Sowerby.

Although the matter, then, was, in some senses, sorted out over 200 years ago, none of the surviving *Actinotus helianthi* specimens discussed above (the most promising being the right-hand specimen of P-JU No. 10408) can be incontrovertibly associated with Labillardière before his publication, so that stability is best served by selecting the only undoubted surviving 'original material' in his protologue, namely the published plate (Fig. 1) as lectotype for the name *A. helianthi*.

This investigation has been concentrated on a single Labillardière species: from our findings above, there would appear still to be further, possibly extensive, work to be done to resolve other geographical anomalies in his Australian taxa - a task beyond the scope of this paper.

Fig. 1. *Actinotus helianthi*. Lectotype (image courtesy Peter Crossing Collection; photograph by Jaime Plaza).

Actinotus helianthi Labill., *Novae Holl. Pl. Spec.* 1: 67 + t. 92 (1805).

Lectotype [icon] **designated here** by M.J. Henwood and D.J. Mabberley: Auguste Plée (engraving, 'Actinotus helianthi'), after Pierre-Antoine Poiteau, in Labill., *Novae Holl. Pl. Spec.* 1.: t. 92 (1805).

Eriocalia major Sm., *Exot. Bot.* 2: 37 + t. 78 (1806). (See Fig. 2)

Lectotype **designated here** by M.J. Henwood and H.W. Lack: New South Wales, Port Jackson, *J. White s.n.* in Herb. Sm. 478.1 (LINN-SM); isolecto: G00415882 (G).

Fig. 2. *Actinotus helianthi* (left) *Eriocalia major*, James Sowerby in J.E. Smith, *Exotic Botany* 2: t. 78 (1806); (right) Unknown engraver after Sowerby in Trattinnick, 'Tabulae' t. [275] (1816?) with added details taken from Ple[acute accent] e's engraving (see Fig. 1).. Courtesy Peter Crossing Collection; photographs by Jaime Plaza.

Note: Sowerby's plate was likely redrawn from a sketch made in New South Wales and sent with a specimen by Surgeon White to Smith's druggist friend, Thomas Wilson (Mabberley 2020a: 92). Trattinnick's plate is a copy, in reverse, of that engraved by Belling after Ignaz Strenzel (see below) copying and 'improving' Sowerby's plate (in reverse) before 1816, as Belling's engraving was published in Trattinnick's much delayed *Thesaurus botanicus* ([1805-] 1819), t. 73 (the only discernible watermarks in the plates of the copy of the book in the Peter Crossing Collection are '1803' – see below).

Actinotus minor

The second New South Wales species to be scientifically described was also first collected by Banks and Solander (BM013717919, BM013717920, BM013717921, with duplicates at the National Herbarium of New South Wales (NSW133686, NSW264211, NSW133497)) but was published even later than was *A. helianthi* - as *Eriocalia minor* Sm. (1806), based on materials (specimens and drawing), sent to England by Surgeon John White, and the published plate by Sowerby. In standard databases, its placement in *Actinotus* is attributed to Candolle's *Prodromus* in 1830, but Leopold Trattinnick, as pointed out by Mabberley (2020a: 349), published the binomial as 'Actinotus minor m[ihi]' before that, and issued an unsigned, coloured engraving copied from Sowerby's drawing for Smith's *Eriocalia minor*:

[1]***Actinotus minor*** (Sm.) Tratt., *Ausg. Taf. Archiv* 3: 47 & t. [216; unsigned] 'Actinotus minor m[ihi].' (1814); Tratt., *Freye Auswahl Pflanzenabbild*. n. 276 (1816) & t. [276] (1816?); DC., *Prodr*. 4: 83 (1830).

Basionym: *Eriocalia minor* Sm., *Exot. Bot*. 2: 39 + t. 79 (1806). (See Fig. 3)

Lectotype **designated here** by M.J. Henwood and H.W. Lack: New South Wales, Port Jackson, *J. White s.n.* in Herb. Sm. 478.2 (LINN-SM); isolectotype: G00415883 (G).

Fig. 3. *Actinotus minor* (left) engraving by James Sowerby in J.E. Smith, *Exotic Botany* 2: t. 79 'Eriocalia minor' (1806); (right) Unknown engraver after Sowerby in Trattinnick, 'Tabulae' t. [276] (?1816). Courtesy Peter Crossing Collection; photographs by Jaime Plaza.

Note: Sowerby's plate was likely redrawn from a sketch made in NSW sent with a specimen by Surgeon White to Smith's druggist friend, Thomas Wilson (Mabberley 2020a: 92).

Trattinnick names of other, largely Australian, plants

Subsequent to this, his first, excursion into Australian botany, and more importantly perhaps, Leopold Trattinnick (also Trattinick, Trattinnik, Trattinik; 1764–1849), later coined completely new names for other Australian plants. These, also neglected, names were largely published on plates, generally pirated as in 'his' *Actinotus* plates discussed and illustrated above. Trattinnick was not the first to work like this, an earlier Central European example centred on an Australian plant being the case of *Acacia verticillata* L'Hér. (Leguminosae/Fabaceae). This was first described in L'Héritier's *Sertum anglicum*: 30 (1789), based on a David Nelson

[1] * = Corrections and additions to APNI and other databases

herbarium specimen collected in Adventure Bay, Tasmania, in 1779 during Cook's third voyage, but the cited plate (as tab. 41) was never published. However, this plate was copied by A.J.G.K. Batsch (1761–1802), an early exponent of the natural system of classification, and appeared as 'Mimosa verticillaris' in the second edition of his *Der geöffnete Blumengarten* (1802; Mabberley 2020a: 336-37).

Trattinnick was a botanist of private means; from 1808 until 1835 he was the first (paid) curator of the newly founded Pflanzencabinett in Vienna (Svojtka 2015), which in 1810 became part of the k[aiserlich] k[önigliche] Vereinigte Hof-Naturaliencabinette then headed by Carl Franz Ritter von Schreibers (Riedl-Dorn 1998: 265). Trattinnick was in a privileged position: he was a member of the Imperial Household and had ready access to books in both the Imperial Library and the private library of Franz I, Emperor of Austria. Moreover, these two libraries and the botanical collections, of which Trattinnick was curator, were all housed in the same building, namely the Hofburg palace in Vienna.

Like Robert Brown, Trattinnick was an early exponent of the Natural System of classification as he set out in his *Genera plantarum* of 1802, an unillustrated work. Trattinnick also produced a whole series of illustrated books. Again, many of the illustrations in these were copied from other works. His *Thesaurus botanicus* ([1805–] 1819) is perhaps his first such 're-use' of the plates of others, those copied including illustrations in Andrews's *Botanist's repository* (1797–1815), Cavanilles's *Icones et descriptiones plantarum* (1791–1801), and Ventenat's *Jardin de la Malmaison* (Mabberley 2020a: 349). Trattinnick's book was planned to be issued in 20 parts of four plates each; the first five numbers were available in 1805, but the rest, reportedly delayed by the 'Napoleonic Pause', not until 1819. The finely coloured engravings are after images redrawn by, among others, Ignaz Strenzel (1786–1832) of the k[aiserlich] k[önigliche] Akademie der vereinigten bildenden Künste in Vienna, and Franz Reinelli (1785–1812), known for flower decoration on porcelain. All the plates of Australian plants figured were 'recycled' images, though some were genuinely 'improved' by the new artists (see *Actinotus helianthi* above).

In 1811, while the *Thesaurus botanicus* was 'paused', Trattinnick published a *Plan eines botanischen Universalwerks, welches unter dem Titel Archiv der Gewächskunde, und in besonderen Unterabtheilungen unter ebenso vielen Titeln erscheinet* [Plan for a botanical work of universal scope, which is published under the title Archiv der Gewächskunde in special subsections with the same number of different titles]. Judging from the subtitle, Trattinnick was aiming this projected work at a broad market, listing 'physicians, surgeons, vets, apothecaries, gardeners, forest officers, farmers, travellers, manufacturers, artists, dyers, educators, statisticians and all those who are interested in botanical knowledge'. This was an ambitious plan (Lack 1981), and resulted in several publications with different titles (among them *Archiv für Gewächskunde,* 1811–18), though the whole project was neither successful nor completed. One of the reasons for its failure was the fact that many illustrations were copies of familiar published images. Furthermore, the *Archiv für Gewächskunde* had uncoloured illustrations, while his *Ausgemahlte Tafeln aus dem Archiv für Gewächskunde* (now an extremely rare book with just three copies traced in public libraries) comprised coloured illustrations, though the associated cheaper price seems not to have made up for that; their plate numbers differ and there are different numbers for individual illustrations.

The rationale behind Trattinnick's plagiarism seems to have been an apparently altruistic motive to make plates in otherwise expensive and inaccessible works available, his going as far as to reduce the prices of his own publications (Mabberley 2020a: 302). However, such discounts may have been as likely acts of desperation because, perhaps in part due to bad business decisions on such ventures, he was depleting his inherited fortune (Wunschmann 1894). In particular, his *Archiv der Gewächskunde* was an attempt (subsidised by himself, the title pages bearing the note 'auf Kosten des Herausgebers' [at the publisher's expense]) to make available, in an inexpensive serial, illustrations of a wide range of plants, by copying most of them from earlier expensive works, using more-than-competent local engravers to copy the plates. In 1816, apparently giving up on the project as originally conceived, Trattinnick issued a prospectus listing, without descriptions, many more plates than he had already published: *Freye Auswahl einzelner Pflanzenabbildungen in schwarzen Kupfern*, pp. [4] with *Index 800 Iconum Plantarum pro libero delectu singularium*. There is a copy, without any obvious provenance, bound with a selection of the issued, unnumbered but named, plates, without title-page or other letterpress, in the Peter Crossing Collection, Sydney. The copper plates are numbered in pencil corresponding to the pencil annotations in the prospectus (the only other recorded surviving copies of the prospectus are in the Herzogin-Anna-Amalia-Bibliothek in Weimar, Germany - shelf mark Ruppert 5182, formerly in the private library of no less than Johann Wolfgang von Goethe, and in the library of Kroměříž, the palace of the archbishop of Olomouc, in Czechia, this copy being filed with four boxes containing 519 unbound plates[ii]): box 1 with 138, box 2 with 136, box 3 with 139 and box 4 with 106 plates.

According to Trattinnick's prospectus, the illustrations were on sale for just one year, after which the plates would be destroyed, but that seems not to have eventuated because, in 1819, the prospectus was reprinted in

two journals, *Jahrbücher der Gewächskunde* and *Isis* to *Litterarischer Anzeiger*, as further advertising. Later it was reprinted yet again in Trattinnick's *Botanisches Taschenbuch* (1821), once more without any descriptive material relating to the individual plates.

Whether or not all 800 plates, which include some which Trattinnick had already published with the same numbers in *Archiv der Gewächskunde*, were issued requires further research in European libraries, but even the selection in the Peter Crossing Collection is revealing. That set has 368 plates bound in more-or-less alphabetical order, annotated with pencil numbers bound in numerical order, but with many gaps, suggesting that the unknown collector, for whatever reason, eschewed binding (or buying) those missing here. Indeed, this set appears to include all those engravings thought at the time to be depicting new plants: the first collector thus seems to have been a discriminating one. Several of those plates unissued beforehand have 'analysis' and therefore their accompanying new names coined by Trattinnick are validly published there, typified by the plates themselves.

Then, in 1821, there appeared Trattinnick's *Auswahl vorzüglich schöner, seltener, berühmter, und sonst sehr merkwürdiger Gartenpflanzen, in getreuen Abbildungen nebst Erläuterungen über ihre Charakteristik, Verwandschaft, Klassification, Geschichte, Verwendung, Cultur, und ästhetischen Ansichten* [Selection of exquisitely beautiful, rare, famous and otherwise very unusual garden plants, in accurate illustrations, together with explanations of their characteristics, relationships, classification, history, use, culture and aesthetic properties] in two volumes, the first with 1–100 unnumbered, uncoloured, engraved plates, the second with 101–200 also unnumbered. This is now a very rare book, but it was intended to continue Trattinnick's efforts to make illustrated botanical works available to a wider audience. There are copies in the State Library of New South Wales, Thüringer Universitäts- und Landesbibliothek Jena, Bayerische Staatsbibliothek München, Universitätsbibliothek Regensburg, and Österreichische Nationalbibliothek Wien. Some plates were drawn by Trattinnick himself, though the artists for many others are unknown, but some are signed and are attributable to Baron Franz Xaver von Eyb (1795–1859), with many engraved by Joseph Seher (1781–1836). Several seem to be the plates listed in the 1816 prospectus and are again copied from published works, notably Smith's *Exotic botany*, e.g. t. 10, James Sowerby's *Dendrobium speciosum* Sm. (Orchidaceae), re-engraved by Seher as Trattinnick's t. [65] (1821), the pair reproduced side by side in Mabberley (2020a: 205).

The copy of this Trattinnick book in the Peter Crossing Collection has descriptions and discussions of plants (more than 40 Australian) depicted in the plates (again numbered in pencil), some of which have drawn anatomical analyses. Volume 1 begins with three species of *Banksia* and later has other Proteaceae besides many South African *Erica* spp., but also 'new' species like *Amaryllis candida* (see below), complete with what is in effect a generic monograph of *Amaryllis*. Trattinnick continued to utilise his stock of plagiarized plates in his *Genera nova plantarum* (1825) and his *Botanisches Album, oder Sammlung ausgewählter naturgetreur Abbildungen* (c. 1850, so perhaps posthumous) with 150 engraved plates, again numbered in pencil.

Trattinnick's botanical papers (and therefore any unsold plates) are lost. According to a file 'Angebot des Nachlasses von Leopold Trattinnick 11. X. 1902 – 10. II. 1912' in the archive of the Österreichische Nationalbibliothek in Vienna, on 11 October 1902 a certain 'Regierungsrätin Prof. Weiss' offered to sell the Trattinnick effects to the Fideikommißbibliothek (FKB), the private library of the imperial family in Vienna. Although the offer was repeated, it was to be turned down on 17 December 1908 because of, among other things, a lack of interest in botanical works and the fact that copies of all of Trattinnick's published books were already in the FKB. On 20 August 1912 the Vienna bookseller Karl Trau tried to sell Trattinnick's miscellaneous papers to the director of the Generaldirektion der k[aiserlich] und k[öniglicher] Familienfonds [general directorate of the imperial and royal family foundation] for 9000 Kronen (perhaps some $200 000 today). This, too, was rejected, on 9 December 1912, because the price was considered exorbitant and, according to the file, Trau, had tried, rather unwisely and clearly unsuccessfully, to bribe the head librarian of the FKB.

The '1816' plates

According to his prospectus, Trattinnick's '1816' plates, were offered for sale as available from 31 December 1816. His very many *Eryngium* plates in the set were cited in 1820 by Karl Sprengel in Schultes, *Syst. Veg.* 6: 316 et seqq., e.g. p. 331 including tt. 763, 764 (*Eryngium humile* even with a new varietal description apparently based on the latter plate); *Hosta japonica* t. 89 was cited by Kunth, *Enum. Plant.* 4: 591 (1843) and at least two more are in IPNI/POWO also as 'Tabulae', that is n. 333: *Amaryllis brasiliensis*, the hybrid between *Hippeastrum reginae* (L.) Herb. and *H. vittatum* (L.Hér.) Herb., the first-raised hybrid *Hippeastrum* (see below) and n. 488: *A. candida* (also see below). Other IPNI 'Tabulae' are *Imperata ovata* tab. 569 and *Primula spectabilis* tab. 426, but both these names were published by Trattinnick before the 1816 plates were issued, unlike those on several plates in the Peter Crossing Collection.

It must be concluded that these plates were in circulation at the time: it stretches the bounds of credulity to consider that, with Trattinnick's extensive networks, besides advertisements in two journals of relatively wide circulation, no more than two sets were printed and distributed, even if they are very rare today. As these plates seem to have been available individually, further surviving examples are likely to be found in collections of prints and drawings, rather than in bound volumes on library bookshelves, though, perhaps surprisingly, none has yet been found in either Staats- und Universitätsbibliothek Göttingen, or Naturhistorisches Museum Wien (Archives, Department of Botany) or Universitätsbibliothek Wien. Nonetheless, three previously unrecognized plates have already been found in the collections of unbound drawings and prints filed in the herbarium 'wings' (not library) at Royal Botanic Gardens, Kew – see *Amaryllis candida* below.

A purist might argue that as the '1816' plates themselves have no reference to the prospectus (except for the numbers added in pencil), the new names should be attributed to the artist and/or engraver on them, rather than to Trattinnick, but some plates, including the two below with new generic names, have neither artist's nor engraver's names, so we have attributed them here to Trattinnick.

The plates with analysis and bearing new names are as follows (with one other unconsidered Trattinnick name added for completeness). Note that *Portenschlagia* Tratt. on two other such plates is a new generic name (= *Elaeodendron* Jacq. (1782)), named after Franz Edler von Portenschlag-Ledermayer (1772–1822), and is generally considered to have been published in 1818 by Trattinnick, but it is represented by these plates (with analysis) figuring *P. australis* Tratt. (n. 250 of the 1816 Prospectus = *E. australis* Vent., Celastraceae), and *P. integrifolia* Tratt. (n. 284 of the Prospectus = *E. australe* var. *integrifolium* (Tratt.) DC.), both from Australia, but it is as yet to be shown that these separate plates were distributed before 1818, either together or at different times.

Akkermannia* Tratt., **A. florida* Tratt., *Freye Auswahl Pflanzenabbild*. n. 286 (1816) & t. 'Ackermannia florida' (?1816); Tratt. in *Jahrb. Gewächskunde* 1: 170 (1819); *Isis, Literr. Anzeiger* 1819: 198 (1819); Tratt., *Bot. Taschenbuch* 1: 331 (1821) = ***Myoporum* Banks & Sol. ex G.Forst., ***M. tetrandrum*** (Labill.) Domin (Scrophulariaceae, Australia). (Fig. 4)

Notes: The generic name[iii] apparently commemorates Trattinnick's printer, Johann Emanuel Akkermann (1764–1836), and antedates both *Ackermannia* Pat. (1902) = *Sclerocystis* Berk. & Broome (Glomeraceae) and *Ackermania* Dodson & R. Escobar (1993) = *Benzingia* Dodson (Orchidaceae). This unsigned illustration, with analysis, was copied, the main figure in mirror image, from Plée after Poiteau in Labillardière, *Novae Hollandiae Plantarum specimen* 1: t. 82 'Pogonia tetrandra' Labill. 1805, so the binomial could be taken to be a nomen superfluum, if use of the same plate is an 'indirect reference' (cf. ICN Art. 41.3), but we are assured that there is insufficient linkage in the prospectus text itself for this to be so (John McNeill in litt. 17 Mar. 2020) and Trattinnick's names are therefore validly published, the plate itself being an iconotype. *Myoporum tetrandrum* is restricted to southwest Western Australia.

Amaryllis candida* Tratt., *Freye Auswahl Pflanzenabb*. n. 488 [2 plates] (1816) & 2 tt. 'Amaryllis candida' (?1816); Tratt. in *Jahrb. Gewächskunde* 1: 175 (1819); *Isis, Literr. Anzeiger* 1819: 198 (1819); Tratt., *Bot. Taschenbuch* 1: 337 (1821); Tratt., *Auswahl Gartenpfl.* 1: 34, 41, tt. [21, 21 bis] (1821, non Lindl. in *Bot. Reg.* 9: t. 724 (1823) = *Zephyranthes candida* Herb. (1826)), = ***Crinum jagus* (J.Thomps.) Dandy (Amaryllidaceae, tropical Africa).

Notes: The unsigned ?1816 illustrations with analysis, engraved by Joseph Seher were copied from Redouté, *Liliacées* 4: t. 181 'Crinum giganteum' Redouté. 1807, so the binomial could be taken to be a nomen superfluum, if use of the same plate is an 'indirect reference' (cf. ICN Art. 41.3), but we are assured that there is insufficient linkage in the prospectus text itself for this to be so (John McNeill in litt. 17 Mar. 2020) and the name is therefore validly published. We are indebted to John David (WSY) for recognising the copied Redouté image of this tropical African plant. There are examples of both of these Trattinnick plates at K (Julia Buckley in litt. 1 June 2021, in response to a recent specific request by DJM to look for them: a third, of *Amaryllis* (i.e. *Nerine*) *sarniensis* L. has subsequently been found – Julia Buckley in litt. 24 June 2021).

Astragalus involucratus* Tratt., *Freye Auswahl Pflanzenabb*. n. 293 (1816) & t. 'Astragalus involucratus' (?1816), Tratt., in *Jahrb. Gewächskunde* 1: 175 (1819); *Isis, Literr. Anzeiger* 1819: 198 (1819); Tratt., *Bot. Taschenbuch* 1: 331 (1821); non Lipsky (1901 = *A. cottonianus* Aitch. & Baker) = ***A. galactites* Pall. (Leguminosae).

Notes: Plate drawn & engraved by Ignaz Albrecht (1759-?) with analysis, perhaps original work. We are very grateful to Andrey Sytin (Saint Petersburg) for this identification.

Baumgartenia* Tratt., **B. sobolifera* Tratt., *Freye Auswahl Pflanzenabbild*. n. 619 (1816) & t. 'Baumgartenia sobolifera' (?1816); Tratt. in *Jahrb. Gewächskunde* 1: 175 (1819); *Isis, Literr. Anzeiger* 1819: 198 (1819); Tratt., *Bot. Taschenbuch* 1: 341 (1821); Tratt., *Auswahl Gartenpfl.* 1: 110, t. [60] (1821); Tratt., *Rosac. Monogr.* 1: 14 (1823) = ***Kalanchoe* Adans.; ***K. pinnata*** (Lam.) Pers. (Crassulaceae).

Notes: A plant native in Madagascar, but an environmental weed in eastern Australia and elsewhere. Undoubtedly the name commemorates Johann Christian Gottlob Baumgarten (1765–1843), botanist resident in Vienna. Unsigned image,

with analysis, copied from Hooker, *Paradisus Lond.* 1: t. 3 'Bryophyllum calycinum' Salisb. 1805, so the binomial could be taken to be a nomen superfluum, if use of the same plate is an 'indirect reference' (cf. ICN Art. 41.3), but we are assured that there is insufficient linkage in the prospectus text itself for this to be so (John McNeill in litt. 17 Mar. 2020) and the names are therefore validly published with the plate itself as iconotype; in *Auswahl*, however, Trattinnick explicitly includes *Bryophyllum calycinum* in the synonymy. Likely antedates *Baumgartenia* Spreng. (1817) = *Borya* Labill. (1805); *Baumgartia* Moench (1794 = *Cocculus* DC. [1817], nom. cons.) also commemorates Baumgarten.

Johannia microphylla* (Bonpl.) Tratt., *Archiv Gew.* 1: 13, t. 82 (1812); Tratt., *Obs.*: 51 (1812); Tratt., *Ausg. Taf. Arch.* 1: n. 8, t. 8 (1813); Tratt., *Freye Auswahl Pflanzenabb.* n. 82 [i.e. same number as in *Archiv*] (1816); F.G.Dietr., *Nachtr. Vollst. Lex.* 4: 126 (1818); *Jahrb. Gewächskunde* 1: 180 (1819); *Isis, Literr. Anzeiger* 1819: 199 (1819); Tratt., *Bot. Taschenbuch* 1: 324 (1821); Tratt., *Gen. Nov.* t. 24 ('Joannia', 1825), based on *Chuquiraga microphylla* Bonpl. = ***C. jussieui* J.F.Gmel. (Compositae).

Note: A medicinal plant native in the Andes of Ecuador and Peru.

Fig. 4. *Myoporum tetrandrum* (left) engraving by Auguste Plée after Pierre-Antoine Poiteau in Labillardière, *Novae Hollandiae Plantarum specimen* 1: t. 82 'Pogonia tetrandra' (1805); (right) engraving (reversed) by unknown artist after Plée in Trattinnick, 'Tabulae' t. 'Ackermannia florida' (?1816). Courtesy Peter Crossing Collection; photographs by Jaime Plaza.

Orchis richardii* Tratt., *Freye Auswahl Pflanzenabbild.* n. 517 ('richardi', 1816) & t. 'Orchis richardi' (?1816); *Jahrb. Gewächskunde* 1: 182 (1819); *Isis, Literr. Anzeiger* 1819: 200 (1819); Tratt., *Bot. Taschenbuch* 1: 331 (1821); Steud., *Nomencl. Bot.*, ed. 2, 2: 224 (1841) = ***Dactylorhiza incarnata* (L.) Soó (Orchidaceae).

Notes: Engraving by Leopold Beyer (1789–1877) after one Weishaupt, with analysis, the same image, as 'Orchis incarnata' in Tratt., *Ausgemahlte Tafeln aus dem Archiv der Gewächskunde* 3: legends p. 27 verso, n. 268, + t. [268] (1814), with analysis and is perhaps original work. Europe. We are indebted to John Grimshaw for confirming the identity of the plant figured in the plate. The link to [L.C.M.] Richard in the specific epithet may well be that *Orchis divaricata* Rich., an unpublished name, was included in the synonymy of *O. latifolia* L. var. *angustifolia* Lois. (= *D. incarnata*) by Loiseleur-Deslongchamps, *Fl. Gallica* 2: 606 (1807), who wrote 'An species distincta?' referring to Richard's collection of *D. incarnata* (P: P00852384) from Saint-Gratien, now a northern suburb of Paris; Richard's binomial was first validated as *O. divaricata* Rich. ex Boreau, *Fl. Centre France* ed. 2: 522 (1849).

Primula hornemanniana* Tratt., *Ausg. Taf. Arch.* 4: 33 & t. 375 (1814), *Freye Auswahl Pflanzenabb.* n. 424 (1816) & t. 'Primula hornemanniana' (?1816) *Jahrb. Gewächskunde* 1: 183 (1819); *Isis, Literr. Anzeiger* 1819: 200 (1819); Tratt., *Bot. Taschenbuch* 1: 335 (1821) = ***P. stricta* Hornem. (Primulaceae).

Notes: An Arctic plant. *Primula hornemanniana* Tratt. antedates *P. hornemanniana* Lehm. (1817), but these two are conspecific. 1814 and ?1816 images are unsigned and are perhaps original work.

Amaryllis × *brasiliensis Redouté (Amaryllidaceae)*

Trattinnick's plate of *Amaryllis* × *brasiliensis* (see above) was a copy of Pierre Josephe Redouté's, itself the iconotype of *Amaryllis* × *johnsoniana* Ker Gawl., which provides apparently the oldest available specific epithet for the name of the well-known St Joseph's Lily, widely grown in Australia and currently known as:

Hippeastrum* × *johnsonii (Gowen) Herb., *Amaryll.*: 142 (1837) (Amaryllidaceae).

Amaryllis* × *johnsoniana* Hort. ex Ker Gawl., *J. Sci. Arts* 1: 177 (1816); J. Murray, *Edinb. Phil. J.* 9: 241 (1823), **syn. nov.

Type [icon] '*Amaryllis brasiliensis*' Redouté, *Liliacées* 8: t. 469 (2 Mar. 1815 ; non Andrews [1804 = *Hippeastrum puniceum* (Lam.) Voss]); Tratt., *Ausg. Taf. Arch.* 4: 18, t. 333a, b (1815?); Tratt., *Freye Auswahl Pflanzenabb.* n. 381 (1816), Tratt., *Jahrb. Gewächskunde* 1: 175 (1820), Tratt., Bot. *Taschenbuch* 1: 333 (1821), non Andrews (1804 = *H. puniceum* (Lam.) Voss).

Amaryllis × *johnsonii* Gowen, *Trans. Hort. Soc.* 4: 498 (1822); Sweet, *Hort. Brit.*: 402 (1826); Bosse, *Vollst. Handb. Blumeng.* 1: 173 (1829); Reider, *Ann. Blumist.* 5: 45 + t. [19] (1829) & *Geheim. Blum.* 3: 43 (1830); Bury, *Select. Hexandr.* Pl. 1: t. 1 (1831).

Type: ? (living plants not preserved?).

Notes: In 1822 Gowen used this name, which was current in nurseries, but could perhaps be considered an orthographic variant of the first-published *A.* × *johnsoniana*, though, as *A. johnsonii* was in use in horticulture before Gawler published, its having been raised by Johnson before 1810, *A.* × *johnsoniana* may have been a lapsus, as that rendering is not recorded as being used in nurseries. *Amaryllis* × *johnsonii* may well have been validly published in some, as yet unrecognised earlier publication, in any case, but it may be wise to conserve the spelling of the specific epithet of this horticulturally important plant in case it was not. In the absence of a specimen, Redouté's plate could be a good candidate for type material. [It is unclear whether or not Reider's publication antecedes Bosse's, as both appeared in April 1829, though '*A. johnsonii*' was being used, at least in correspondence, by Bosse from at least 1825 (see *Verhandlungen des Vereins zur Beförderung des Gartenbaues* 2: 379. 1826)].

Amaryllis × *regina-vittata* Gowen, *Trans. Hort. Soc.* 4: 498 (1822), nom. illegit.

Note: Possibly just an indication of parentage rather than an intended alternative binomial, as *A. johnsonii* is otherwise used throughout his article.

Amaryllis × *carnarvonia* DC., *Pl. Rar. Jard. Genève*: 30, t. 9 (1825); van Geel, *Sertum bot. fasc.* 14 (1829).

Lectotype [icon] **here designated** by H.W. Lack and D.J. Mabberley: Hippolyte Millenet (engraving 'Amaryllis Carnarvonia' after Jean Christoph Heyland), in DC., *Pl. Rar. Jard. Genève*: 30, t. 9 (1825).

Notes: Since all specimens of this hybrid cultivated in the Geneva Botanical Garden and now preserved in G were collected several years after the publication of the protologue, the plate is apparently the sole candidate for lectotype, though a monographer might choose to designate one of those G specimens as an epitype.

This, the first hybrid *Hippeastrum* ever to be synthesised, was reportedly raised in England by watchmaker Arthur Johnson, of Prescot in Lancashire (a town famed for watchmaking in the eighteenth and nineteenth centuries) before 1810 and named after him (cf. Baker, *Amaryll.* 1888: 57). It has been grown in the Royal Botanic Garden Sydney since 1828, when it was introduced by the superintendent, Charles Fraser (c. 1788–1831).

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References

Brown R (1832) Remarks on the structure and affinities of *Cephalotus*. *London and Edinburgh Philosophical Magazine and Journal of Science* 1: 314–317. https://www.biodiversitylibrary.org/item/53496#page/332/mode/1up

Burdet HM (1979) *Auxilium ad botanicorum graphicem*. Editions des Conservatoire et Jardin botaniques de la Ville de Genève. Publ. hors-série 2. (Conservatoire et Jardin botaniques, Geneva)

Callmander MW, Durbin OD, Lack H-W, Bungener P, Martin M, Gautier L (2017) Etienne-Pierre Ventenat (1757–1808) and the gardens of Cels and Empress Joséphine. *Candollea* 72: 87–132. https://doi.org/10.15553/c2017v721a8

Chappill JA, Wilkins CF, Crisp MD (2008) Taxonomic revision of *Gompholobium* (Leguminosae: Mirbelieae). *Australian Systematic Botany* 21: 67–151. https://doi.org/10.1071/SB07030

Chevalier A (1953) Un grand voyageur naturaliste normand: J.-J. La Billardière (1755–1834). *Revue Internationale de Botanique Appliquée et Agriculture Tropicale* 32: 97–124. https://doi.org/10.3406/jatba.1953.6573

Diment JA, Humphries CJ, Newington L., Shaughnessy E (1983) Catalogue of the natural history drawings commissioned by Joseph Banks on the *Endeavour* Voyage 1768–1771 held in the British Museum (Natural History). Part 1: Botany: Australia. *Bulletin of the British Museum (Natural History), Historical Series* 11: 1–183. https://doi.org/10.5962/p.310430

Duyker E (2000) Ventenat, Abbé Louis (1765–1794). Pp. 1786–1788 in *Dictionaire de biographie mauricienne.* (Port Louis, Société de l'histoire de l'Ile Maurice)

Duyker E (2003) *Citizen Labillardière: a naturalist's life in revolution and exploration (1755–1834)*. (Miegunyah Press, Melbourne)

Duyker E (2005) A French garden in Tasmania: the legacy of Félix Delahaye (1767–1829). Pp. 21–35 in Cropp G et al. (eds) *Pacific journeys: essays in honour of John Dunmore.* (Victoria University Press, Wellington, New Zealand) https://www.isfar.org.au/wp-content/uploads/2016/10/37_EDWARD-DUYKER-A-French-Garden-in-Tasmania-the-Legacy-of-Felix-Delahaye-1767-1829.pdf

Emery NJ, Henwood MJ, Offord CA, Wardle GM (2017) Right here, right now: populations of *Actinotus helianthi* differ in their early performance traits and interactions. *Austral Ecology* 42: 367–378. https://doi.org/10.1111/aec.12450

Freer S (2003, trans.) *Linnaeus's Philosophia botanica*. (Oxford University Press, Oxford)

Henderson RJ (1983) Plants of Australia. Pp. 128–177 in Carr DJ (ed.) *Sydney Parkinson. Artist of Cook's Endeavour voyage*. (Croom Helm, Beckenham, England)

Jeandet A (1883) Notice sur la vie et les travaux de Leschenault de la Tour. *Bulletin de la Société des Sciences Naturelles de Saône-et-Loire* 2: 123–158. https://books.google.com.au/books?id=ftMW5T4hV0YC&printsec=frontcover#v=onepage&q&f=false

Jones OS (2017) A lasting legacy: The Baudin expedition in Australian waters (1801–1803). *The Great Circle* 39: 56–85.

Jouanin C (1997) La passion de la nature ou Joséphine amateur et mécène des sciences de la nature. Pp. 20–34 in Anon., *L'impératrice Joséphine et les sciences naturelles.* (Paris, Éditions de la Réunion des musées nationaux)

Lack HW (1981) 72. Leopold Trattinnick: Ausgemahlte Tafeln aus dem Archiv für Gewächshauskunde. Pp. 156–157 in Lack, HW, Becker, PJ, Brandis, T (eds) *Staatsbibliothek Preussischer Kulturbesitz. 100 Botanische Juwelen. 100 Botanical Jewels* (= *Staatsbibliothek Preussischer Kulturbesitz Ausstellungskataloge* 30). (Reichert, Wiesbaden)

Letouzey Y (1989) *Le Jardin des Plantes à la croisée des chemins avec André Thouin, 1747–1824*. (Muséum National d'Histoire Naturelle, Paris)

Mabberley DJ (1985) *Jupiter botanicus: Robert Brown of the British Museum*. (Cramer, Braunschweig; British Museum (Natural History), London)

Mabberley DJ (1988) Meliaceae. Pp. 17–89 in Morat, P, MacKee, HS (eds), *Flore de la Nouvelle-Calédonie et Dépendances 15*. (Muséum National d'Histoire Naturelle, Paris)

Mabberley DJ (2017) The plates. Pp. 20–295 in Gooding M, Mabberley DJ, Studholme J, *Joseph Banks' Florilegium: botanical treasures from Cook's First Voyage*. (Thames & Hudson, London & New York)

Mabberley DJ (2020a) *Botanical Revelation: European encounters with Australian plants before Darwin. The Peter Crossing Collection*. Reprint with corrections. (NewSouth, Sydney)

Mabberley DJ (2020b). Friedrich Dietrich v. Kurt Sprengel: and their, largely, American plant-names. *Journal of the Botanical Research Institute of Texas* 14: 241–253. https://doi.org/10.17348/jbrit.v14.i2.1005

Mabberley DJ, †Moore DT, assisted by Wajer J (2021, in proof). The Robert Brown Handbook: a guide to the life and work of Robert Brown (1773–1858), Scottish botanist [*Regnum Vegetabile 160*]. (Koeltz Botanical Books, Glashütten, Germany)

Nelson EC (1974) The locations of collections and collectors of specimens described by Labillardière in '*Novae Hollandiae Plantarum Specimen*' – Additional notes. *Papers and Proceedings Royal Society of Tasmania* 108: 159–170. http://dx.doi.org/10.26749/rstpp.108.159

Nelson EC (1975) The collectors and type locations of some of Labillardière's "Terra Van-Leeuwin" (Western Australia) specimens. *Taxon* 24: 319–336. https://doi.org/10.2307/1218341

Nelson EC (1976) Antoine Guichenot and *Adenanthos* (Proteaceae) specimens collected during Baudin's Australian expedition. *Journal of the Society for the Bibliography of Natural History* 8: 1–10. https://doi.org/10.3366/jsbnh.1976.8.1.1

Riedl-Dorn C (1998) *Das Haus der Wunder. Zur Geschichte des Naturhistorischen Museums in Wien*. (Holzhausen, Vienna)

Stafleu FA (1966) Labillardière, 'botanist-voyageur'. Pp. v–xxxxi in Labillardière, J-J, *Novae Hollandiae plantarum specimen* [reprint; Cramer J, Swann, HK (eds) *Historiae naturalis classica* 45]. (Cramer, Lehre)

Svojka M (2015) Trattinnick (Trattinick, Trattinnik, Trattinik) Leopold, Botaniker. Pp. 428–429 in *Österreichisches Biographisches Lexikon 14*. (Böhlau, Vienna) https://doi.org/10.1553/0x00326e95

Ventenat EP (1803–1805) *Jardin de la Malmaison,* vol. 1–2. (Paris) https://www.biodiversitylibrary.org/item/139922#page/9/mode/1up

Weston PH (1994) The Western Australian species of subtribe Persooniinae (Proteaceae: Persoonioideae: Persoonieae). *Telopea* 6: 51–165. https://www.biodiversitylibrary.org/item/264631#page/55/mode/1up

Willson EJ (1961) *James Lee and the Vineyard Nursery Hammersmith*. (Hammersmith Local History Group, London)

Worrall R, Offord CA, von Richter LV (2004) Flannel flower. Pp. 433–441 in Salvin S, Bourke M, Byrne T (eds) *The new crop industries handbook*. (Rural Industries R&D Corporation Publication 04/125) https://www.agrifutures.com.au/wp-content/uploads/publications/04-125.pdf

Wunschmann E (1894) Trattinnick, Leopold. Pp. 498–499 in *Allgemeine Deutsche Biographie* 38 (Duncker & Humblot, Leipzig)

Endnotes

[i] According to James Edward Smith, champion of the Linnaean system of classification (Lady Smith, *Memoir and correspondence of the late Sir James Edward Smith, M.D*. 2: 457 (1832), "M. La Billardière has disposed his book according to the system of Linnaeus, a rare example in France, where any thing not French usually comes but ill recommended."

[ii] "[HWL] I presume that the Trattinnick plates were acquired by no less than Archduke Rudolf, from 1819 archbishop of Olomouc, cardinal in Rome, friend of Beethoven and dedicatee of several of his more important works. He died in 1831 in Baden in the Eisenstädter Haus, almost certainly looked after by Anton Rollett, town physician, a relative of mine and whose visitors book has Trattinnick's signature".

[iii] Trattinnick was wont to name new genera after colleagues – in the Linnaean tradition: "According to [Linnaeus's] Philosophia botanica (1751) 238. Generic names that have been formed to perpetuate the memory of a botanist who has done excellent service should be religiously preserved. This, the only and pre-eminent reward for such labour……" (Freer 2003: 185). Such included *Baumgartenia* Tratt. (see above); *Brownetera* Rich. ex Tratt., Gen. Nov. Pl.: t. [14]. 1825, nom. illeg., superfl. pro *Podocarpus* Labill. = *Phyllocladus* Rich. ex Mirb. (Podocarpaceae), after Robert Brown (Mabberley & Moore 2021), *Dietrichia* Tratt. [1814] (= *Crassula*, Crassulaceae) after Friedrich Dietrich (1768-1850); Mabberley, 2020b), *Hosta* Tratt. [1812] (Asparagaceae; the only of his such names recognised today, after Nicolaus Thomas Host (1761–1834), *Lehmannia* Tratt. (1824, non Spreng., 1817 = *Nicotiana* L., Solanaceae), = *Argentina* Hill (Rosaceae), after Johann Georg Lehmann (1792–1860); *Portenschlagia* Tratt. (see above); *Roemera* Tratt. [1802], (non *Roemeria* Medik. [1792], Papaveraceae) = *Steriphoma* Spreng. (Capparaceae), after Johann Jacob Römer (1763–1819) though not indicated thus in the protologue; *Schmidtia* Tratt. [1816] = *Coleanthus* Seidl (Gramineae/Poaceae), after Franz Willibald Schmidt (1764–1796); *Ventenatia* Tratt. [1802] = *Euphorbia* L. (Euphorbiaceae) after Étienne Pierre Ventenat (1757-1808). Trattinnick himself is commemorated in *Trattinnickia* Willd. (Burseraceae [tropical South America], 1806), '*Trattenickia*' Pers. (1807) being *Marshallia* Schreb. (Compositae).

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